POPULATION ECOLOGY OF CARIBBEAN ASCOGLOSSA (MOLLUSCA: OPISTHOBRANCHIA): A STUDY OF SPECIALIZED ALGAL HERBIVORES

KERRY B. CLARK AND DUANE DeFREESE
DEPARTMENT OF BIOLOGICAL SCIENCES
FLORIDA INSTITUTE OF TECHNOLOGY
MELBOURNE, FLORIDA 32901, U. S. A.

ABSTRACT

Ascoglossan (= Sacoglossan) populations were sampled in fifteen habitats in Florida, Belize, and Bermuda. Thirty-seven species were collected, with a maximum of thirteen species in a single habitat. Ascoglossan communities of these habitats were compared via Czekanowski's similarity coefficient. Several broad habitat types were described based on dominant vegetation, sediments, and water quality: epimanglic, epilithic, subtropical lagoon, coral-sand, and coral reef. Ascoglossan associations for most of these habitats were distinctly separable, with similarity coefficients ranging from about 75% to 20%.

Lower population densitites (biomass and number of individuals g^{-1} dry algae) occurred on coral reefs than in mangrove areas. Population density increased with latitude. Population density also decreased as dietary ash level increased.

Ascoglossan populations have potential as indicators of environmental quality, feeding on algae that occur primarily in clear water of low to moderate nutrient availability and low sediment load. Life histories and morphology of prey algae could represent adaptations to varied nutrient regimes; these life history patterns entrain those of their ascoglossan predators. Species that have high density populations and irruptive life histories generally feed on septate, seasonal algae, while low-density, stable species feed on perennial siphonaceous algae. Highly calcified algae appear resistant to ascoglossan feeding; low feeding rates could have been a strong force favoring evolution of kleptoplasty (= symbiotic chloroplasts).

The Ascoglossa are unusual animals, possessing several unique specializations. They are perhaps the most stenotrophic of marine herbivores, feeding suctorially on a wide range of marine plants (Clark and Busacca, 1978). They have highly adaptive reproduction, with a notably high incidence of encapsulated metamorphosis and lecithotrophy (Clark and Goetzfried, 1978; Clark and Jensen, 1981). Also, they are the only animals known to support "symbiotic chloroplasts" (kleptoplastids), which provide direct solar carbon fixation (Trench, 1975). Unfortunately, we know relatively little about their ecology, perhaps due to major problems in quantitative sampling (discussed below). As a result, the functions of these animals in marine ecosystems are poorly understood.

Although trophically specialized, ascoglossans as a group are broadly distributed in latitude and habitat, and exhibit a variety of life history patterns. This combination of dietary specialization with otherwise broad adaptation is uncommon among marine animals, and suggests that detailed study of life histories of ascoglossans could provide information of general interest in marine ecological theory. A paucity of data on ascoglossan populations, however, limits interpretation of their ecological significance and adaptations.

Ascoglossans are, together with herbivorous fish, the major predators of the siphonalean algae, which are the dominant primary producers in coral reef ecosystems [up to 80% of total reef calcium carbonate is produced by the genus *Halimeda* (Goreau and Goreau, 1973; Hillis-Colinvaux, 1986)]. Although the population densities of ascoglossans in the reef environment appear low, their role in reef ecology is potentially significant. An analysis of ascoglossan populations in tropical systems could greatly clarify their ecological importance.

In this study, we present quantitative population estimates from Florida and Belize, C.A., and compare these with population data from other regions. In evaluating these data, we also include descriptions of representative ascoglossan habitats and communities of the subtropical and

tropical Caribbean province.

MATERIALS AND METHODS

Quantitative samples were collected from mangrove cays and the barrier reef near Carrie Bow Cay, Belize, C.A. and from several locations in Florida (Figs. 1, 2). Quantitative sampling generally involved a period of qualitative presampling of potential habitats and algal foods (concentrating on Siphonales, Siphonocladales, and Cladophorales), using snorkel or SCUBA. In this phase we attempted to identify "optimal" habitats as evidenced by high-density populations and the presence of mature animals. During this phase, potential algal foods were detached from the substrata and vigorously shaken underwater. The approximate numbers and species of slugs detached were noted. Evidence of feeding (evacuated algal cells and thalli) and presence of ascoglossan egg masses were typically used to locate potential study populations, but we attempted to analyze all macrophytic algae belonging to the above groups in each of the habitats. To ensure comprehensive surveys of community composition, we spent a minimum of 30 hr presampling in each study area, with total field observation time in Belize of about 300 hr and about 150 hr in Bermuda, each made during two visits. Florida observations represent cumulative studies since 1968 at various sites, with most sites studied on a monthly basis for several years.

Communities were compared on the basis of co-occurrence of species using Czekanowski's similarity coefficient (Clifford and Stephenson, 1975).

Populations from the selected microhabitats were quantified by collecting all slugs detached by the above method, using individual suction collectors (Clark, 1971) for each sample. In the case of growths of filamentous algae (e.g. *Cladophora*) we detached masses of algae containing slugs and separated slugs and eggs in the laboratory. Water temperature was measured with a stem thermometer *in situ*. After each handful of algae was processed, it was stored in a mesh collecting bag. On return to the laboratory, each algal
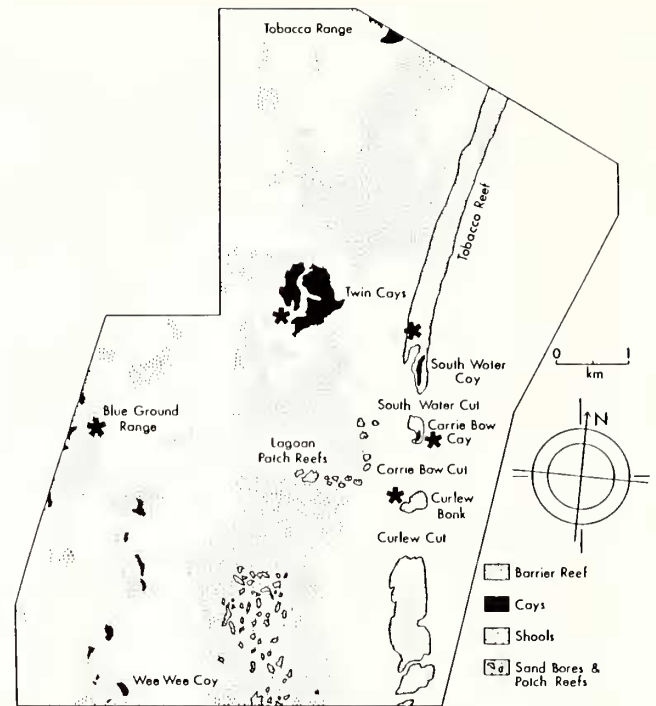

Fig. 2. Vicinity of Carrie Bow Cay, Belize and Twin Cays (from Rützler and Macintyre, 1982).

sample was again examined for slugs possibly missed during the underwater sampling. Slugs were sorted by species, egg masses were removed if present, and slugs and eggs were counted, placed in pre-weighed foil cups, and dried. Algal samples were placed in aluminum foil pans and dried. Belizean samples were partially dried in air or a warm gas oven to prevent decomposition. All samples were dried at 80°C to constant weight before final weighing, following return to our laboratory. Portions of "anchored" siphonales (*Penicillus, Caulerpa* spp., *Udotea*) that are not used as food by ascoglossans were removed to equalize comparisons with other algae (e.g. Cladophorales) in which the entire thallus is utilized as food (Fig. 3). In general, portions with exceptionally tough cell walls [*Caulerpa paspaloides* (Bory) Greville basal stolon and lower stalk] or heavily calcified (white/yellow) portions were removed. In the less differentiated *Caulerpa* species [*C. racemosa* (Forsskål) J. Agardh, *C. verticillata* J. Agardh] the entire thallus' contents appear usable as food, and we used the entire plant in weight determinations. In many locations, slugs can be qualitatively collected but densities are below levels at which algae can be reasonably processed with our present technique (less than one animal per 100 g algal dry weight).

To facilitate comparison of quantitative data based on algal displacement volume or net weight, we have converted other investigators' data to approximate equivalent dry weights using Floridan congeneric algae, rinsed briefly in fresh water and oven dried at 80°C to constant weight. Data for *Limapontia capitata* (Mueller) (Jensen, 1975) were converted from displacement volume to dry weight using
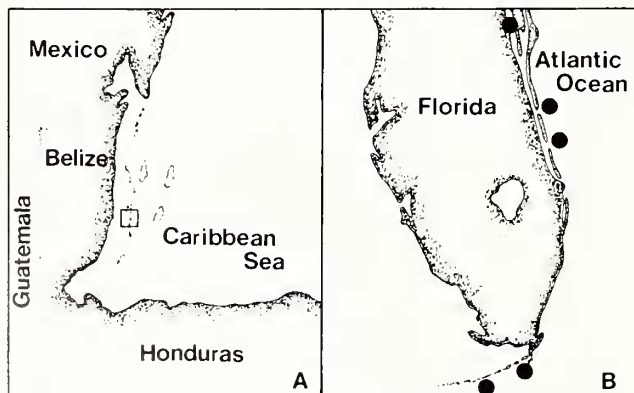

Fig. 1. Locations of principal collection sites in this study. **A.** Belizean barrier reef system. **B.** Eastern Florida, from north to south: north Indian River; Sebastian Inlet; Fort Pierce Inlet; Key Largo; Long Key.
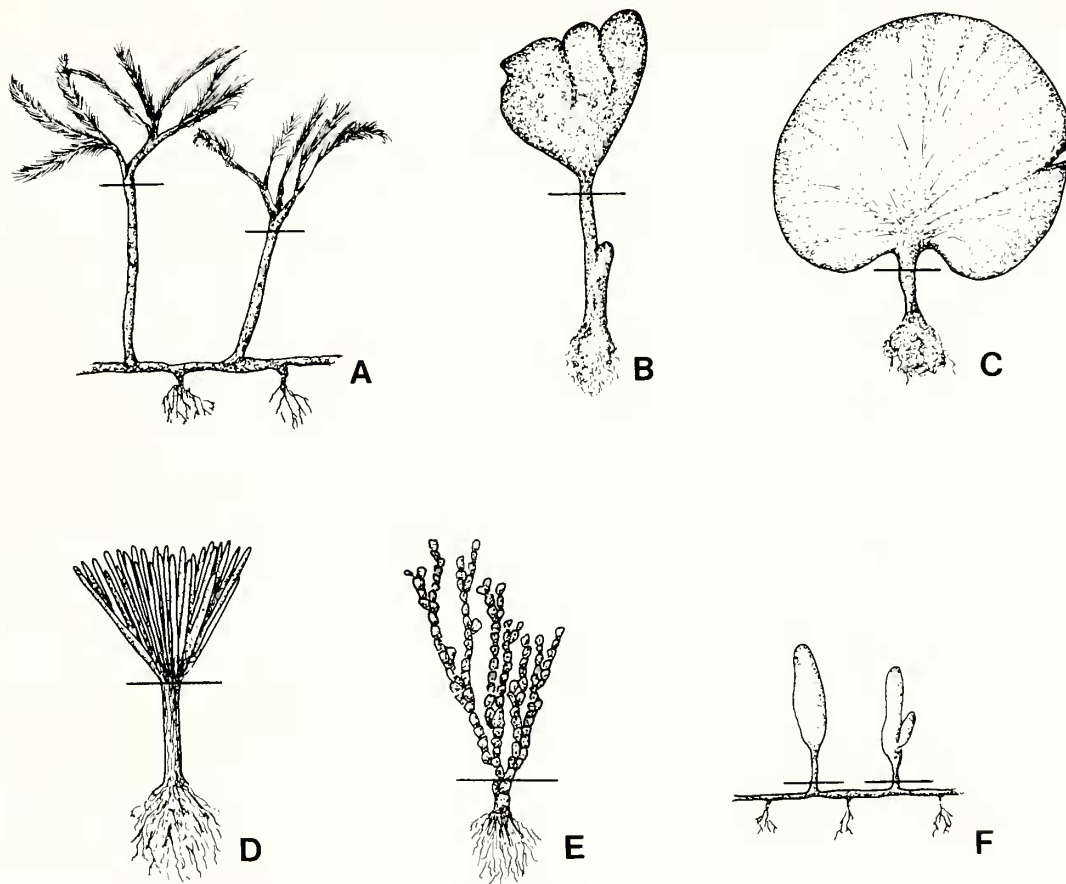
Fig. 3. Selection of tissues (distal to line) used in algal biomass and ash measurements. **A.** *Caulerpa paspaloides.* **B.** *Avrainvillea nigricans.* **C.** *Udotea conglutinata.* **D.** *Penicullus dumetosus.* **E.** *Halimeda incrassata.* **F.** *Caulerpa prolifera.*

Cladophora gracilis (Griffiths ex Harvey) Kützing, collected at Pineda Causeway, Rockledge (0.074 g dry/ml); data for *Elysia furvacauda* Burn (Brandley, 1984) were converted from displacement volume to dry weight using *Codium isthmocladum* Vickers from Sebastian Inlet (0.063 g/ml), and data for *Oxynoe antillarum* Mörch (Warmke and Almadovar, 1972) were converted from wet to dry weight using *Caulerpa racemosa* from Fort Pierce Inlet (0.051 g dry/g wet).

Ash weights were determined using oven-dried algae combusted in a muffle furnace at 500°C.

Model II regression lines were calculated by Bartlett's three group method (Sokal and Rohlf, 1981).

RESULTS

CARIBBEAN ASCOGLOSSAN HABITATS:

The known habitats of ascoglossans in the greater Caribbean province fall into several general types, and can be grouped on the basis of substrata (composition, grain size, and orientation), water quality (nutrient content, wave exposure or water flow), light level, and algal cover (which appears to relate strongly to the above characteristics). These habitat types are broadly distributed and have relatively similar ascoglossan faunae. The habitats are briefly described below, together with their characteristic ascoglossan species (Table 1). We indicate apparent (unmeasured) nutrient conditions based on color, clarity, and source of waters as: oligotrophic (tropical oceanic water of exceptional clarity); mesotrophic (estuarine or coastal water of slight turbidity, usually associated with well-oxidized sediments); eutrophic (water with visible tannin/humate content, sediments usually moderately to heavily organic, associated with mangrove drainage).

VERTICAL ROCK FACE *CAULERPA* ZONE (VRFC):

Common occurrences of this habitat (Fig. 4) include artificial jetties constructed as protection for navigation; natural equivalents also occur as nearshore fossil reefs from Sebastian Inlet, FL south to approximately Boca Raton, and at the outer margins of small bays in Bermuda. Waters are usually oligotrophic to slightly mesotrophic. *Caulerpa racemosa* is the dominant alga in this community, and typically occurs as a restricted band just below the low tide line, mixed with other algal species (most often *C. mexicana* (Sonder) Kutzing and *C. sertularioides* (Weber-van Bosse) Børgesen. Extent of this community can be limited by piscine herbivory, and the VRFC
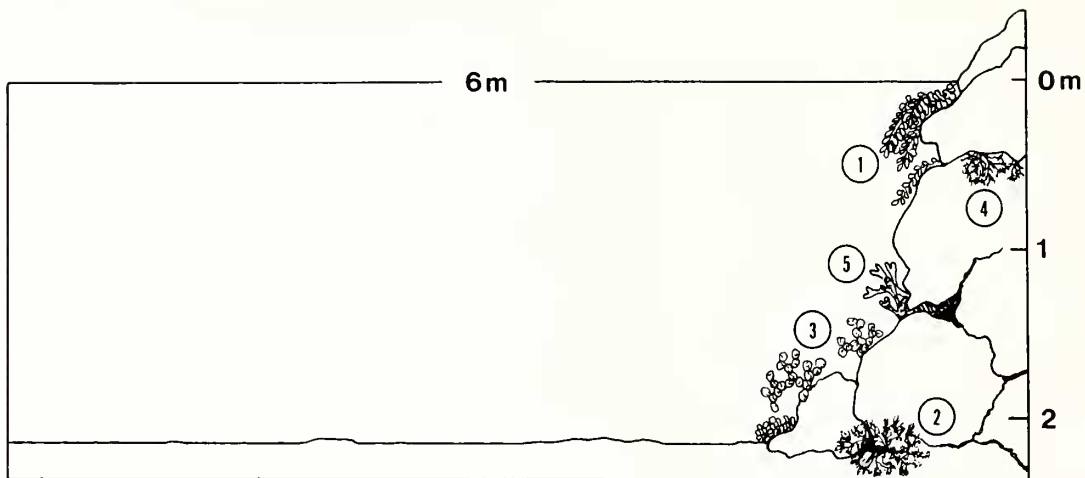
Figs. 4-15. Representative habitats of Caribbean Ascoglossa. Some figures represent composites of several similar habitats (for specific occurrences of individual species, refer to Table 1). Some macrophytes are included for purposes of habitat description only, and are noted as "no ascoglossans". Macrophytes are not to scale. **Fig. 4.** Vertical Rock Face *Caulerpa*, High Energy (Sebastian Inlet, Fort Pierce Inlet, Bermuda Coastal Margins): 1 = *Caulerpa racemosa, C. sertularioides: Ascobulla ulla, Lobiger souverbiei* Fischer, *Oxynoe antillarum, Elysia subornata, Volvatella bermud*ae Clark; 2 = *Cladophora prolifera* (Roth) Kützing: *Aplysiopsis zebra* Clark; 3 = *Halimeda discoidea: Elysia tuca, Bosellia mimetica, Cyerce antillensis;* 4 = *Bryopsis plumo*sa (Hudson) C. Agardh: *Caliphylla mediterranea, Elysia ornata, Placid*a kingstoni Thompson; 5 = *Codium: Placida* sp. (non *dentritica*).

is usually absent in coral reef areas. For example, in Bermuda, the rock faces at the south side of Castle Harbour are completely cleared of macrophytes by intense scarid grazing.

Sebastian Inlet: The winter low temperature apparently prevents establishment of *Halimeda*, but this is a significant component in more tropical examples of the VRFC. *Caulerpa* at Sebastian Inlet is strongly seasonal, usually disappearing from December through March, with a mid-summer dieback as salinity falls with summer rains (to below 20 $^o/_{oo}$ after heavy rain). This habitat is restricted to the north inner jetty, perhaps by climatic effects or by extreme wave action and sediment abrasion on the outer jetties. The inner jetty is protected from heavy natural waves, but boat wakes generate frequent waves of low amplitude (1-3 dm) and there is a strong current (1-2 km/hr) for much of the tidal cycle.

Fort Pierce Inlet: Wave energy is more moderate here, and the *Caulerpa racemosa* belt extends into a sandy beach at the landward edge. There are protected tide pools, shaded and buffered against heavy surf, and these are also colonized by *Bryopsis*, with dense tufts of this alga in spring and after summer upwelling events (Smith, 1982). As previously noted (Jensen and Clark, 1983), this site contains the northernmost representatives of the tropical fauna, with *Elysia tuca* Marcus and *Ascobulla ulla* (Marcus and Marcus), *Bosellia mimetica* Trinchese, and the caliphyllids *Cyerce antillensis* Engel and *Caliphylla mediterranea* Costa; these have not been observed at Sebastian Inlet, about 50 km north. The more tropical nature of Fort Pierce is also evidenced by the occurrence of *C. racemosa* year-round in most years.

A series of fossil algal reefs parallels the shoreline at Ft. Pierce, and these appear to support a similar community. However, high wave energy has made exploration of these difficult.

Bermuda: The VRFC habitat occurs at the outer margins of small bays, with relatively sparse *Caulerpa* growth and qualitatively lower ascoglossan densities than Florida, and along the Bermudan causeways where there is strong current flow and somewhat higher animal densities (not quantified). There are also heavy growths of *C. racemosa* on the rock walls inside of Harrington Sound near submarine caves, associated with zones where groundwater from the caves mixes with seawater.

Florida Keys: Borrow pits (made by quarrying limestone, "borrowed" for highway construction) and marina canals commonly support variations of the VRFC community (Fig. 5). Borrow pits usually have restricted water exchange (with narrow inlets and flow only at high tide), no wave action, and a distinct thermocline is often present. When a thermocline exists, the bottom water is eutrophic and sometimes hypoxic; above the thermocline, where most opisthobranchs occur, the water is mesotrophic. *Caulerpa racemosa* grows in a looser, less compact form than in more exposed VRFC habitats, and a diverse and dense community of ophiuroids, polychaetes, anemones and other invertebrates is associated with the *Caulerpa* and rock crevices. *C. verticillata* is also a major component of these borrow pits and canals. High densities of *Tridachia crispata* Mörch occur in borrow pits and canals but are seldom associated with any particular alga.

Coral-Sand (CS): This habitat (Fig. 6) occurs where layers (2-40 cm) of carbonate sand usually overlie a limestone base, usually at depths of less than 2 m (the lower limit is usually bounded by a *Sargassum*/gorgonian zone). Sediments are typically coarse and well oxidized. Algal cover includes many of the genera of chlorophytes that are principal foods of ascoglossans, including *Halimeda, Udotea, Penicillus, Rhipocephalus, Avrainvillea,* and *Caulerpa*. Thicker sediment

layers accumulate in local depressions in the limestone, and these are usually dominated by *Thalassia testudinum* Banks ex König; with decreasing sediment grain size and increasing organic content, seagrasses replace the algae, and the typical CS community appears as a mosaic of siphonalean algae and seagrasses. Slow to moderate water currents (<0.5 km/h) and oligotrophic to mesotrophic waters characterize these areas.

Upper Florida Keys: The best example of this community occurs at Point Elizabeth at the mangrove fringe, and supports a notably high diversity of ascoglossans at moderate densities.

Middle Florida Keys: Long Key, Spanish Harbor Key. Both sites are near bridges that cross channels, and these

areas are well-flushed by tidal currents, especially Spanish Harbor (Fig. 6). High densities of *Elysia subornata* Verrill, *E. tuca,* and *E. papillosa* Verrill occur here seasonally (Table 2).

Lower Florida Keys (Big Pine Key, Geiger Key): Algae here are shorter and less densely spaced than at Key Largo, and animal densities are generally lower; however, this habitat supports the only known population of *Mourgona germaineae* Marcus and Marcus.

Ferry Reach, Bermuda: This area has finer sediments and a reduced algal diversity relative to the Florida Keys and Belize.

Blue Ground Range, Belize: This habitat occurs around many smaller cays among the Blue Ground Range, but densities of ascoglossans are very low except near
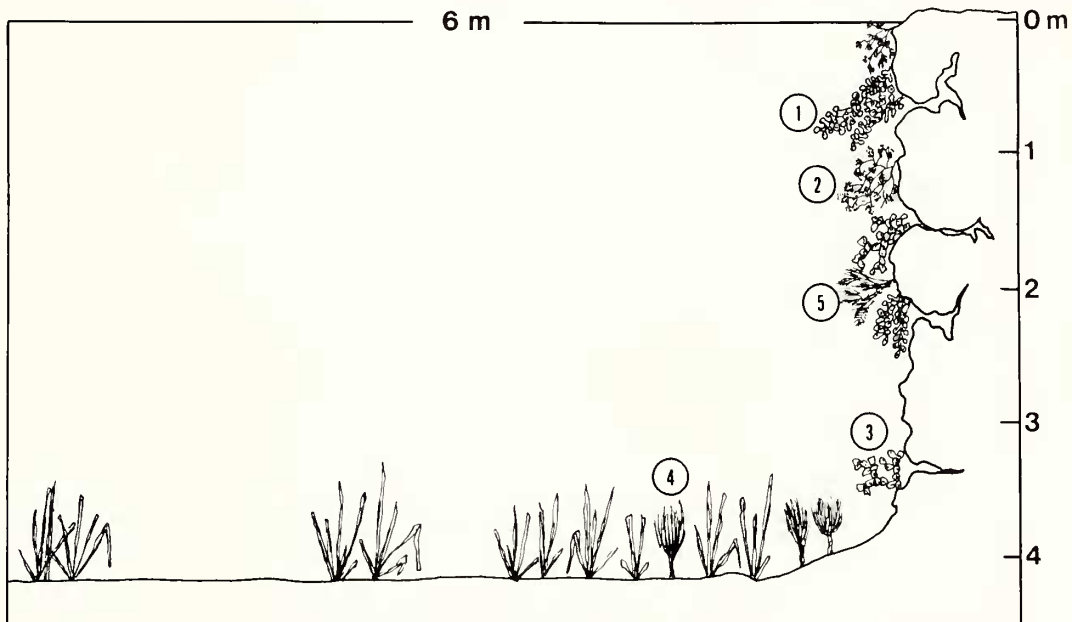
Fig. 5. Vertical Rock Face *Caulerpa,* Low Energy (Florida Keys Borrow Pits, Bermuda Causeways): 1 = *Caulerpa racemosa: Ascobulla ulla, Oxynoe antillarium, Elysia subornata, E. ornata;* 2 = *Caulerpa verticillata: Tridachia crispata* (juveniles), *E. subornata;* 3 = *Halimeda incrassata, H. discoidea: Bosellia mimetica, E. tuca;* 4 = *Penicillus dumetosus* (Lamouroux) Blainville: *Cyerce antillensis;* 5 = *Bryopsis: Placida kingstoni, Elysia ornata.*
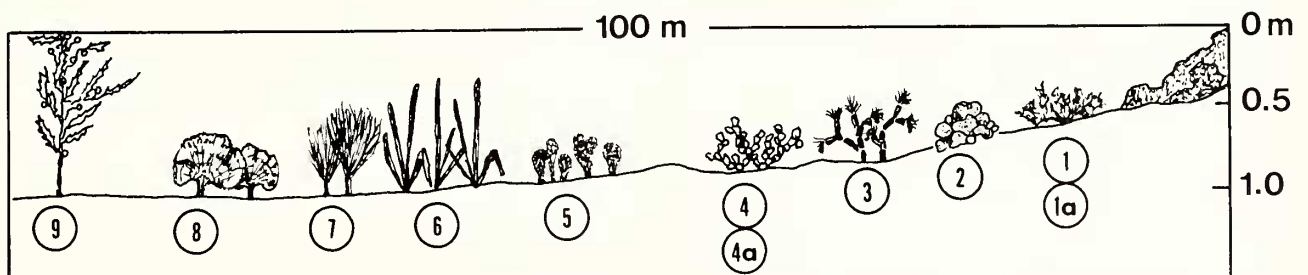
Fig. 6. Coral-sand (Point Elizabeth, Key Largo, FL; Long Key; Geiger Key; Spanish Harbor Key; Blue Ground Keys, Belize; Ferry Reach, Bermuda): 1 = *Cladophoropsis: Ercolania funerea, E. coerulea* Trinchese; 1a = *Caulerpa verticillata: Tridachia crispata;* 2 = *Dictyosphaera: Ercolania coerulea;* 3 = *Cymopolia barbata* (L.) Lamouroux: *Mourgona germainiae;* 4 = *Halimeda incrassata/H. discoidea: Elysia tuca, E. papillosa;* 4a = *Halimeda monile, H. tuna: Cyerce antillensis, Bosellia mimetica;* 5 = *Avrainvillea nigricans: Costasiella ocellifera* (Simroth), *C. nonatoi* Marcus and Marcus; 6 = *Thalassia testudinum: E. serca;* 7 = *Penicillus dumetosus: Elysia tuca, E. papillosa, Cyerce antillensis, E.* n. sp.; 8 = *Udotea conglutinata* (Ellis and Solander) Lamouroux: *E. papillosa;* 9 = *Sargassum* spp. (no ascoglossans); 10 = *Caulerpa paspaloides, C. cupressoides: E. subornata, Oxynoe azuropunctata* Jensen, *Lobiger souverbiei.*
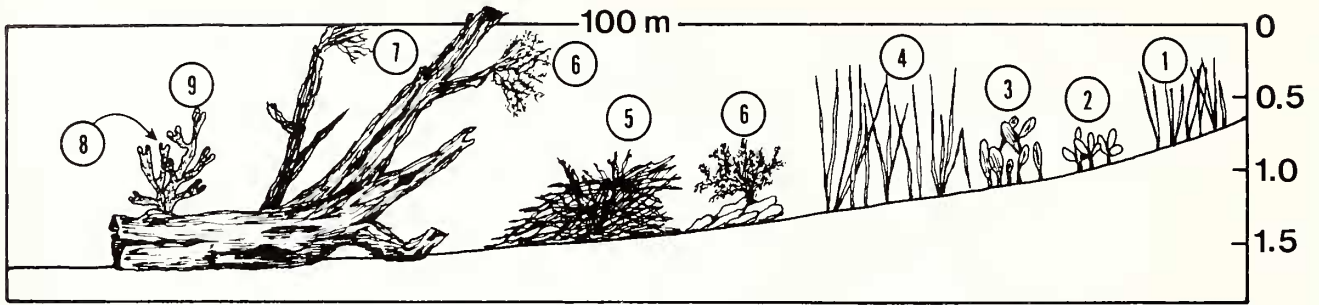
Fig. 7. Northern Indian River Lagoon: 1 = *Halodule wrightii* Ascherson: *Elysia serca;* 2 = *Halophila: E. serca;* 3 = *Caulerpa prolifera: E.* n. sp. "AF"; 4 = *Syringodium filiforme* Kützing (no ascoglossans); 5 = *Drift algal substrates (e.g. Acanthophora)—Chaetomorpha* sp.: *Ercolania funerea;* filamentous Rhodophyta: *Hermaea cruciata* Gould; 6 = *Bryopsis: Ercolania fuscata* (Gould), *Placida kingstoni, Cladophora* sp.: *Ercolania fuscata;* 7 = *Polysiphonia* sp.: *Ercolania fuscovittata* (Lance); 8 = Epiphytic diatoms (on *Codium): Elysia evelinae* Marcus; 9 = *Codium isthmocladium: Placida* sp., *Elysia canguzua* Marcus. Diet unknown: *E. chlorotica* Gould.

mangrove-colonized shorelines. Qualitatively, however, these areas are very similar to areas in the Florida Keys.

Man-O'War Cay, Belize: This small mangrove cay is a rookery; the water up to 50 m from the island has an odor of guano, suggesting a high nutrient content. There is a rich growth of *Bryopsis* extending from below the mangroves to about 40 cm depth, followed by a dense meadow of *Caulerpa racemosa* to about 1 m. In June 1985, we found a great mass of *Chaetomorpha*, estimated at a volume of 23 m³, containing a total of four *Ercolania funerea* (Costa).

SUBTROPICAL BARRIER-ISLAND LAGOON: In sub-
tropical Florida, barrier islands enclose a long salt lake, the Indian River Lagoon. In its undisturbed state, examples of which are unfortunately disappearing rapidly, the Indian River Lagoon received most nutrient input via a very restricted watershed and very limited oceanic exchange, with production dominated by seagrasses and apparently a near-equilibrium of production and respiration. The balance of production and respiration is evidenced by a fine silica sand bottom of low organic content (Gilbert and Clark, 1981). Currents are slow and wind driven except near inlets (von Zweck and Richardson, 1980). Temperature varies widely and rapidly on both diurnal and seasonal scales because of the high surface area: depth ratio of the lagoon (Smith, 1983). Salinity varies with rainfall, and is highest at the end of the dry season. In recent years, much of the lagoon has moved toward a high-turbidity system with increased nutrient influx accompanying urbanization and agricultural expansion, and the seagrasses are steadily declining.

The ascoglossans of the northern Indian River Lagoon (Sebastian to Haulover Canal) are represented in Fig. 7, a composite of species observed since 1972 in this habitat. Two significant changes have occurred during this period; in the absence of prior data, we are unable to determine whether these are permanent or cyclic changes. From 1972 to about 1976, *Chaetomorpha* was a dominant alga in the lagoon and was heavily colonized by *Ercolania funerea* (Costa); at the Haulover Canal in Titusville in 1973, for example, we were able to collect thousands of slugs simply by scooping handfuls of algae into a bucket. In later years, however, the abun-

dance of the alga steadily declined and today the alga occurs as only as isolated threads and small clumps in drift algal masses in most of the areas where it was formerly abundant. A second noteworthy change is the colonization of the North Indian River by *Caulerpa prolifera* (Forsskål) Lamouroux circa 1980. Absent from this part of the river in 1975 (Gilbert and Clark, 1981), *C. prolifera* now forms patches in the sandy bottom at a depth of about 0.5-1.0 m; an undescribed *Elysia*, morphologically similar to *E. subornata* Verrill, eats this alga and occurs from Sebastian to Titusville.

MANGROVE CHANNEL FLOOR (MCF): This habitat occurs in mature mangrove areas in which channels have eroded the peat foundation, sometimes producing a soft, organic mud/silt substrate; waters are mesotrophic to highly eutrophic, depending upon the extent of mangrove drainage. In the best-developed MCF habitats, mature mangrove canopy provides partial or complete shading, and the extent of drainage produces a moderate tidal flow; in some locations, a sand bottom could be present. The peat walls of the channel often support growth of *Caulerpa verticillata*.

Key Largo, Lake Surprise (Fig. 8): Drainage from mangrove areas feeds through Jewfish Creek and into a tidal roadside canal; this canal empties into the Lake Surprise Lagoon onto a delta about 1 m deep. Sediments are partly organic, partly calcareous silt with some shell chaff. *Caulerpa paspaloides* and *Halimeda incrassata* (Ellis and Solander) Lamouroux dominate in patches between the mangrove fringe and the *Thalassia* beds; "islands" of dense patches (1 m diameter) of *Avrainvillea nigricans* Decaisne occur near the mangrove fringe. The roadside canal itself is colonized by some *Thalassia* and *Penicillus*, but like the Twin Cays channel floors described below, has a depauperate ascoglossan fauna, possibly because of the high silt load. A well-developed epimanglic community is present at the mangrove fringe, described separately below.

Twin Cays, Belize, Main Channel (Fig. 9). In broader parts of the channel, the sediment is fine calcareous sand/silt. The diversity of algae and slugs is low here, and densities were too low to sample.

Twin Cays, Hidden Creek (Fig. 10): Sediment here is
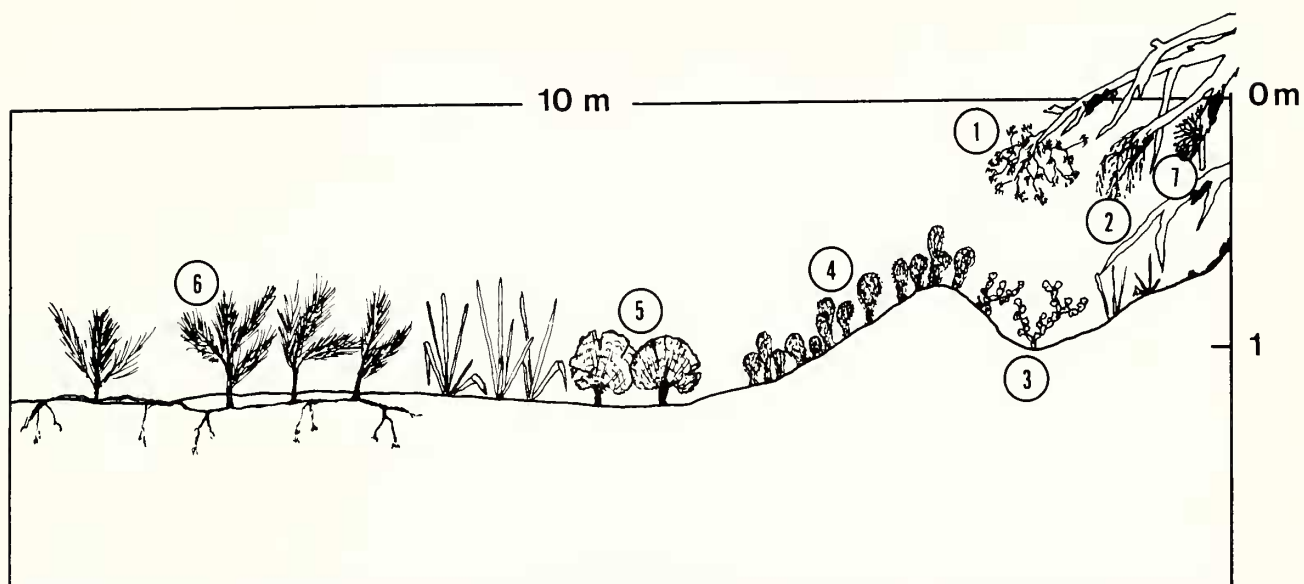
Fig. 8. Mangrove Fringe, Lake Surprise, Key Largo, Florida (Epimangle, Tidal Canal, Mangrove Channel Floor and Delta): 1 = *Caulerpa verticillata: Elysia subornata;* 2 = *Cladophoropsis* sp.: *Ercolania funerea;* 3 = *Halimeda incrassata: Elysia tuca;* 4 = *Avrainvillea nigricans: Costasiella ocellifera;* 5 = *Udotea conglutinata: Elysia patina;* 6 = *Caulerpa paspaloides: Oxynoe azuropunctata, Elysia subornata, Ascobulla ulla;* 7 = filamentous Rhodophyta: *Hermaea cruciata.*
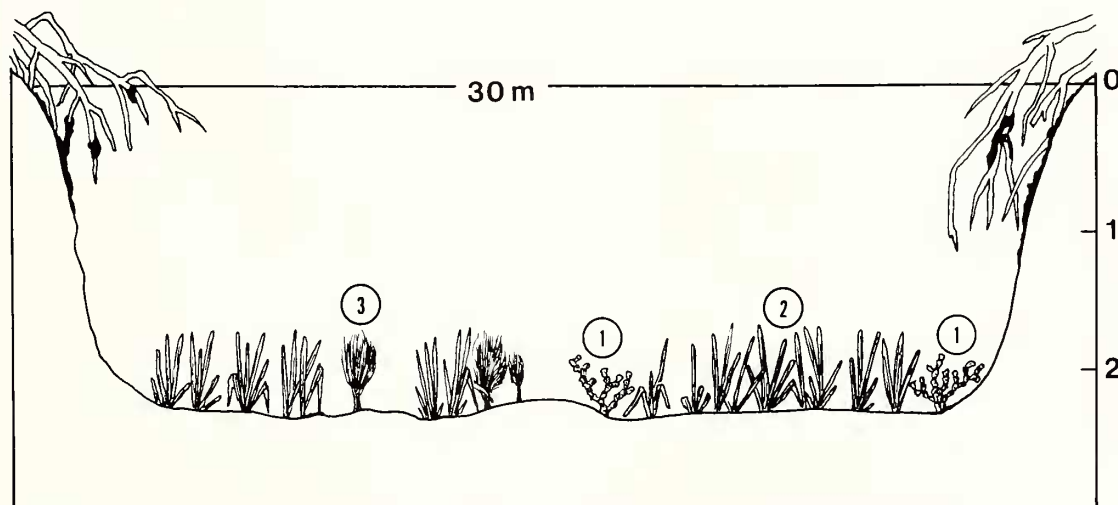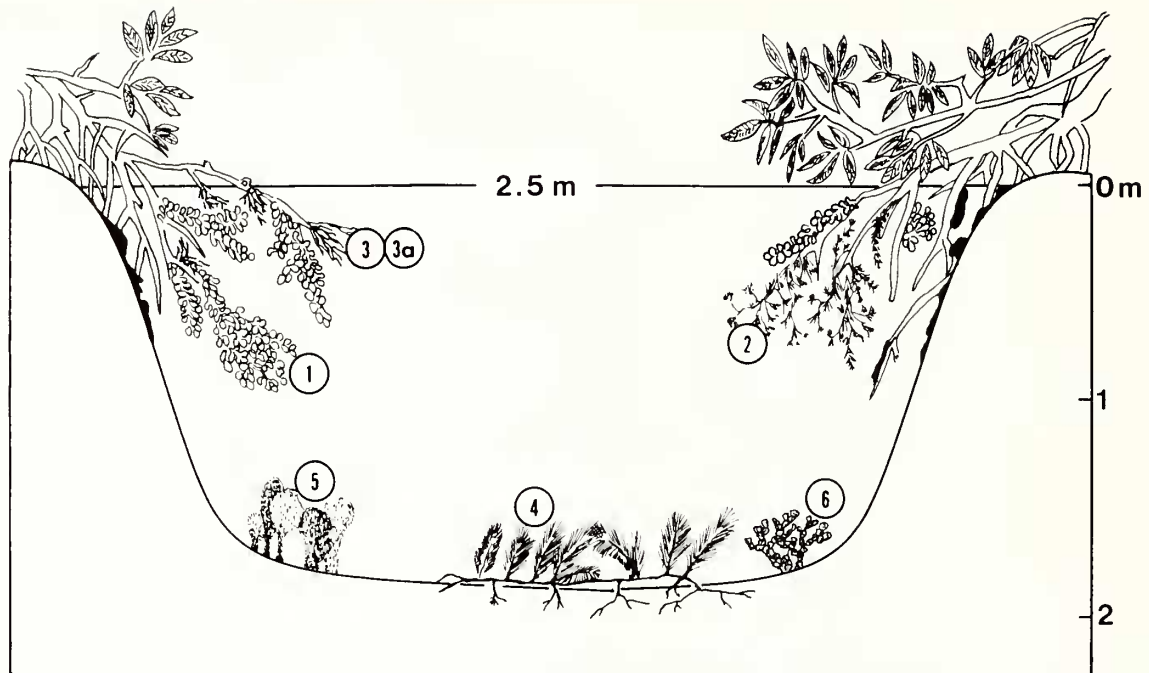

Fig. 9. Mangrove Channel Floor, Twin Cays Main Channel, Belize: 1 = *Halimeda incrassata: Elysia tuca;* 2 = *Thalassia testudinum: Elysia serca;* 3 = *Penicillus capitatus* Lamarck: not colonized.

soft, flocculent, and highly organic. The water is rich in dissolved organic matter draining from shallow mangrove areas in the interior of the island, and reaches high temperatures (34°C in June 1985) if tides ebb in late afternoon. As in the main channel, algae of the channel floor are sparsely colonized, except at ridges at the mouth of the channel, or in patches of algae located at channel junctions.

CHANNEL EPIMANGLE (EPM): Buttress-roots of *Rhizophora mangle* L. extend along the banks of mangrove channels, at times to a depth of >1 m. These buttresses sup-

port dense growths of *Caulerpa* just below the surface, particularly where partially shaded by the *Rhizophora* canopy (Fig. 10). Algae here are isolated from most silt of the channel floor, and support a diverse and moderately dense community of ascoglossans. Optimal conditions appear to occur in narrow, deep channels with high flow and complete shading, as in Hidden Creek and Grouper Garden Channel, Twin Cays. This habitat is poorly represented in most of the Florida Keys, where mangroves are often more fringing growths in shallow water and there is a poor development of epimanglic algae.

Fig. 10. Mangrove Channel Epimangle and Channel Floor (Twin Cays—Hidden Creek, Grouper Garden): 1 = *Caulerpa racemosa: Elysia subornata, Ascobulla ulla, Volvatella bermudae, Lobiger souverbiei;* 2 = *Caulerpa verticillata: Berthelinia caribbea* Edmunds; 3 = *Cladophoropsis: Ercolania coerulea;* 3a = *Bryopsis: Placida kingstoni;* 4 = *Caulerpa paspaloides: Oxynoe azuropunctata;* 5 = *Avrainvillea nigricans: Costasiella ocellifera;* 6 = *Halimeda* spp.: *Bosellia mimetica.*
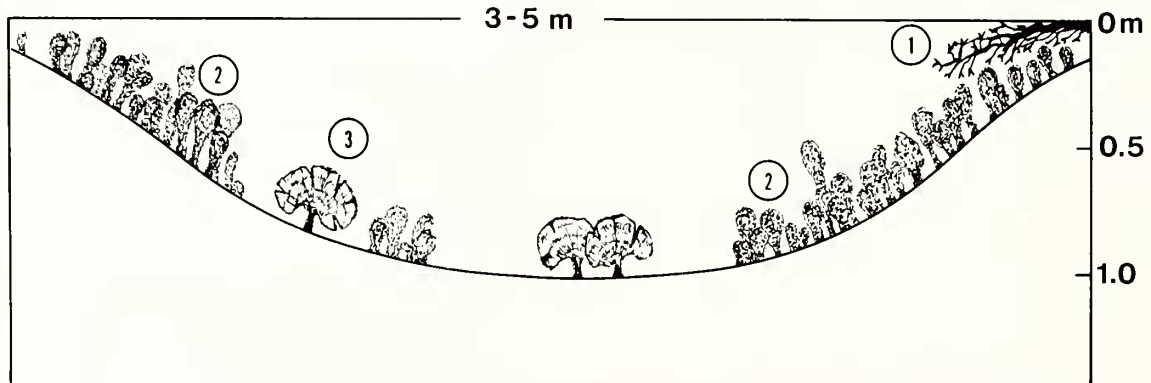
Fig. 11. Mangrove Pond Floor, Twin Cays: 1 = *Acanthophora spicifera* (Vahl) Bøgesen (no ascoglossans); 2 = *Avrainvillea nigricans: Costasiella ocellifera, C. nonatoi; Udotea conglutinata: Elysia patina, E. subornata.*

MANGROVE POND FLOOR (MPF): Twin Cays (Fig. 11): In the interior of Twin Cays, broad, shallow ponds (50-100 m x <0.5 m) form at the end of major channels, apparently via decomposition of mangrove peat. The bottoms of these are largely decomposed peat, but some sandy patches occur. There are sparse patches of *Avrainvillea* and *Udotea*, but high densities (Table 2) of ascoglossans occur on these algae.

BACK REEF FLAT/REEF CREST (BRC): The substrate here is limestone with a thin layer of sediment localized in depressions; water is oligotrophic and a nearly constant flow crosses the BRC. Algal growth is dense, but often closely cropped by fish, especially the uncalcified algae (e.g. *Caulerpa* spp.), and forms an algal turf in areas near the leeward reef crest (Lewis, 1985).

Southwater Cay, north end (Fig. 12): The reef crest here is broader than at Carrie Bow Cay and the back reef is deeper (2-3 m), with higher densities of slugs.

Carrie Bow Cay (Fig. 13): Much of the back reef flat here is quite shallow (<0.5 m in most areas) and exposed to surf for part of each tidal cycle. Most of the ascoglossans here feed upon *Halimeda* spp.; *Elysia serca* Marcus is ap-
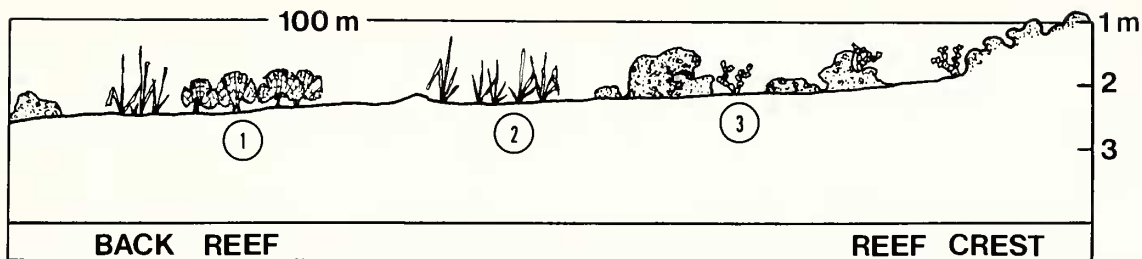
Fig 12. Back reef/reef crest, Southwater Cay, Belize: 1 = *Udotea conglutinata: Elysia papillosa, E. tuca*; 2 = *Thalassia testudinum: Elysia serca*; 3 = *Halimeda incrassata: E. tuca, Elysia* n. sp.
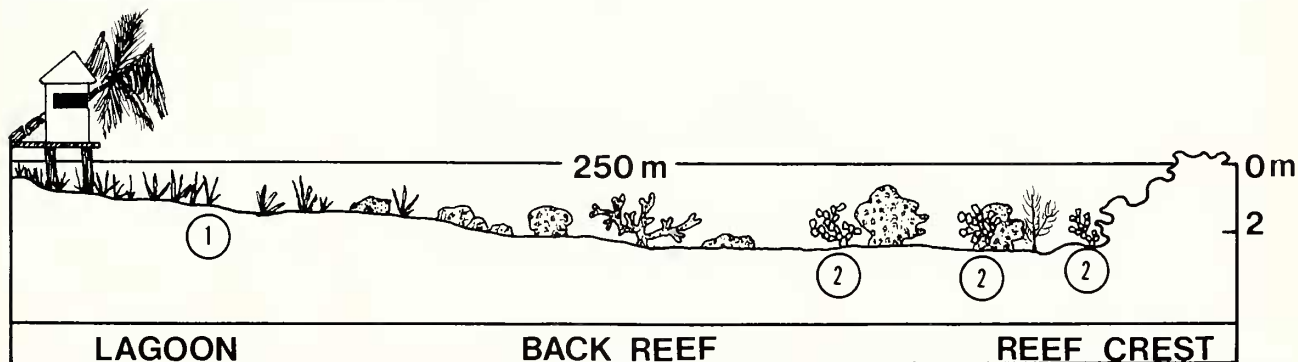
Fig. 13. Back Reef Flat/Reef Crest, Carrie Bow Cay, Belize: 1 = *Thalassia testudinum:* no animals; 2 = *Halimeda* spp.: *Elysia tuca, E. flava, Tridachia crispata, Elysia* n. sp., *Bosellia mimetica.*
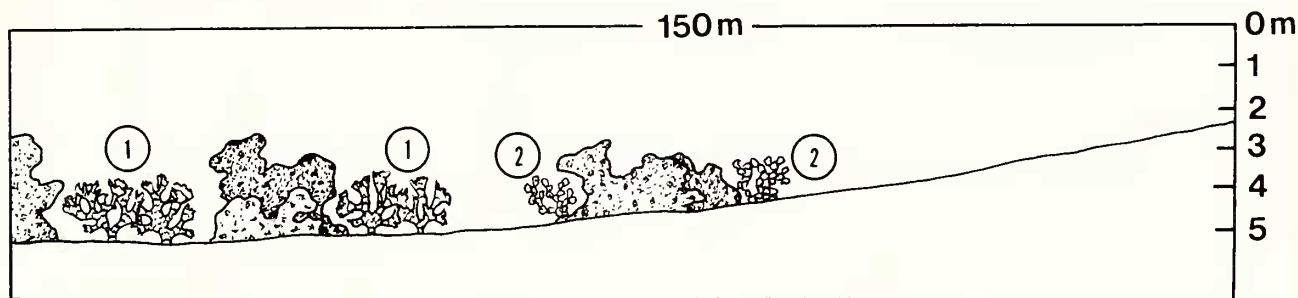
Fig. 14. Curlew Bank Back Reef, Belize: 1 = *Stypopodium zonale* (Lamouroux) Papenfuss (epiphytes): *Elysia tuca, E. papillosa*; 2 = *Halimeda incrassata: Elysia tuca, E. subornata, Bosellia mimetica.*
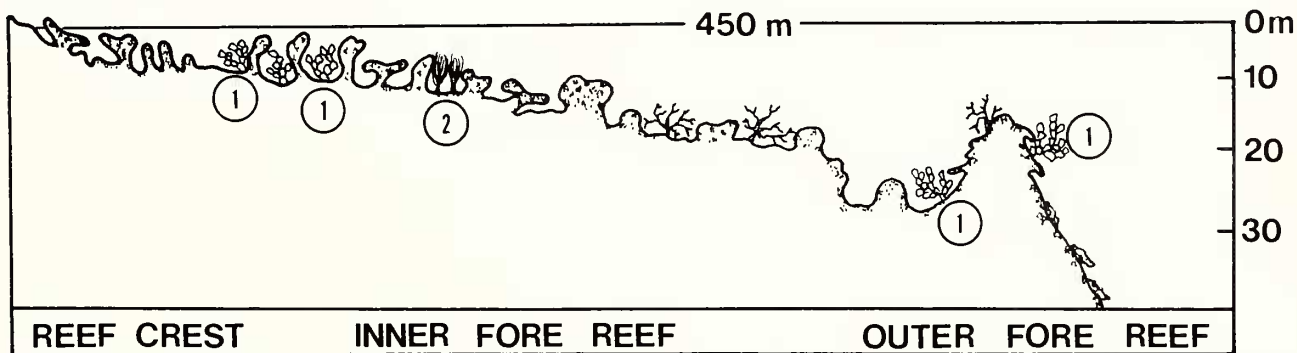
Fig. 15. Reef Crest, Inner Fore Reef, and Outer Fore Reef, Carrie Bow Cay, Belize: 1 = *Halimeda discoidea, H. Simulans* Weber-van Bosse: *Bosellia mimetica, Elysia flava, Elysia* n. sp. "BL", *Tridachia crispata, E. papillosa*; 2 = *Penicillus dumetosus: Cyerce antillensis, E. papillosa.*

parently absent from the *Thalassia*, possibly due to strong currents.

Deep Back Reef, Curlew Bank: The reef crest at this site has eroded, and the back reef slopes rapidly to about 5 m depth (Fig. 14). Two *Elysia* species are associated with the dominant alga *Stypopodium*, apparently feeding on a fine growth of epiphytes on the surface of this alga; these slugs occur in moderate densities but we were unable to quantitatively sample these because of the difficulty of separation of epiphytes from *Stypopodium* thalli. The sand/rock bottom supports few macrophytic chlorophytes other than *Halimeda incrassata*.

Fore Reef/Reef Slope, Carrie Bow Cay (Fig. 15): Algae in this zone are primarily epilithic, with little sediment available for rhizoid attachment. Animal densities are notably lower here, with samples from the fore reef slope below measurable density in most places. Samples from the slope, examined in the laboratory, often had moderate numbers of *Bosellia* juveniles, but these were not quantified.

HABITAT COMPARISONS

Habitats investigated in this study are compared in a trellis diagram based on similarity coefficients (Fig. 16). In general, these habitats are quite distinct, with most associations sharing less than 75% of their species. Three of the Belizean communities are the most distinct (<30%), apparently because the number of species in these habitats (mangrove pond floor, coral-sand, and fore-reef slope) is very low relative to most other communities. The Indian River Lagoon is also quite distinct (32% similarity) from other Caribbean communities, reflecting the presence of several temperate species absent from other Caribbean habitats. The
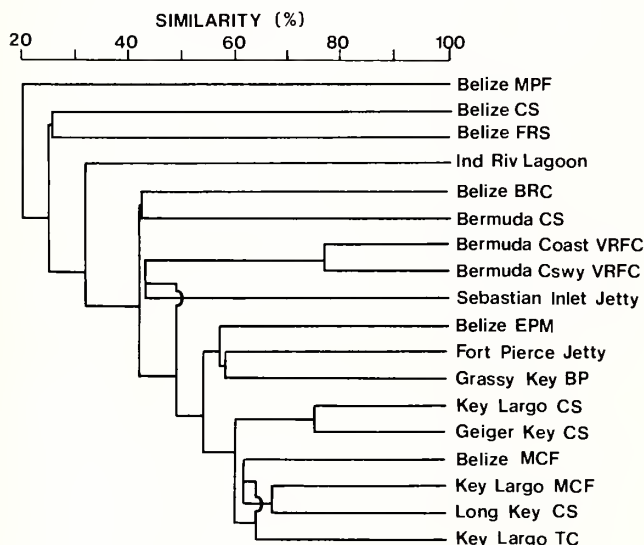
greatest similarity is shown by communities of similar type separated by short distances (Largo and Geiger CS, and Bermuda coastal and causeway VRFC).

Most ascoglossans appear to be highly specialized in habitat selection, with about three-fourths of the species occurring in less than thirty percent of the habitats studied (Fig. 17).
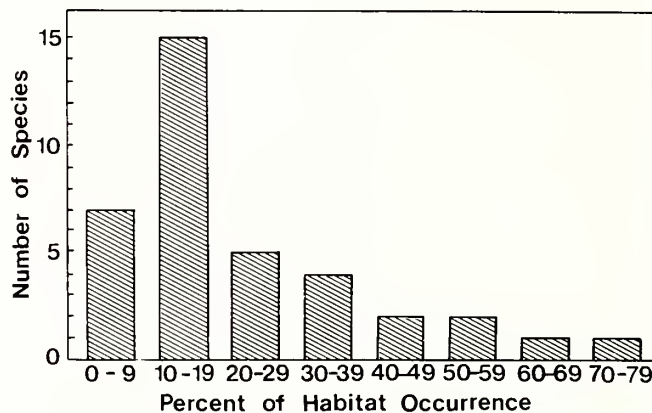
Fig. 17. Habitat selectivity of Caribbean ascoglossans among fifteen habitats.

FAUNAL DENSITIES AND BIOMASS RATIOS:

Densities (animals per unit of algal biomass) and biomass ratios (total animal weight per unit algal weight) are summarized in Table 2. Peak density strongly correlates with latitude when all species are grouped (Fig. 18).

The two major subgroups of the data set, elysiids and stiligerids, were further compared by analysis of covariance (ANCOVA). Residual variance (F = 1.55) and slopes (F = 0.76) of the two families did not significantly differ, but intercepts of the two groups did differ (F = 9.34; d.f. = 1, 16; p<.01). However, at the sample size of the stiligerid and elysiid data subsets, the relationships between density and latitude are not significant (stiligerids: r = .59 with 9 d.f.; elysiids: r = .59 with 6 d.f.).

Higher densities were found in Belizean mangrove habitats than in reef habitats (log transformation; Student's t = 1.79 with 12 d.f., p<.05; mean mangrove density = 0.218/g; mean reef density = 0.028/g). The mean biomass ratio of mangrove areas (0.00178) was greater than that of reef areas (0.00085) but the difference was not significant (log transformation; t = 0.70 with 10 d.f.).

Differences in species composition of the mangrove and reef areas are also distinct (Table 1), with 17 species in the combined mangrove habitats (mangrove channel floor, epimangle, and mangrove pond floor) and eight species in the combined back reef/fore reef; only five species co-occur in both mangrove and reef areas (*Tridachia crispata, Elysia subornata, E. tuca, Bosellia mimetica, Cyerce antillensis*).

Peak biomass ratios increased with latitude (Fig. 19), indicating that high-latitude algae support higher standing stocks of ascoglossan slugs than do more tropical algae. An

Fig. 16. Trellis diagram of similarity of Caribbean ascoglossan communities. Abbreviations: MPF: mangrove pond floor; CS: Coral-sand; FRS: fore-reef slope; LBRC: back reef/reef crest; VFRC: vertical rockface *Caulerpa*; EPM: epimangle; BP: borrow pit; MCF: mangrove channel floor; TC: tidal canal.
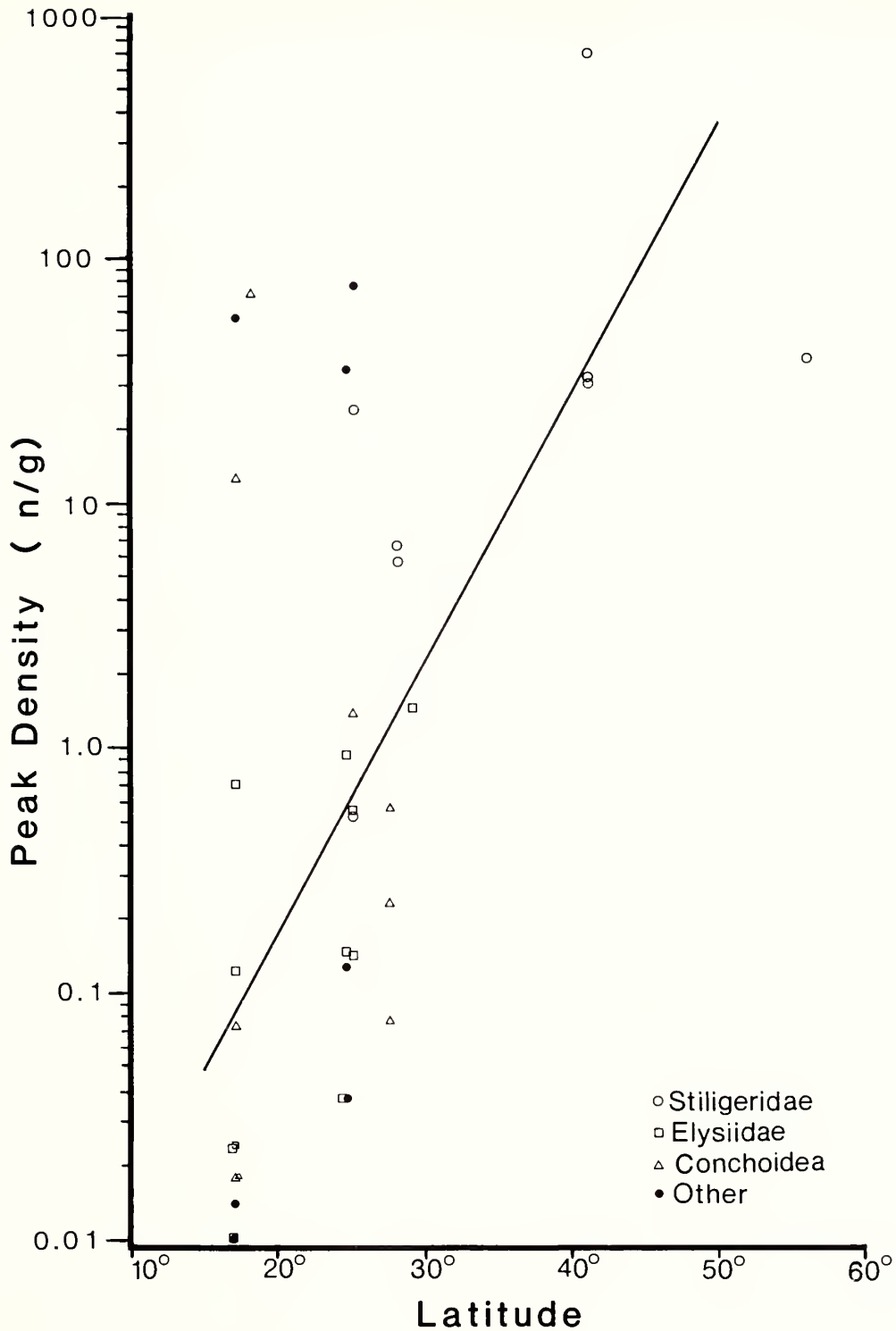
Fig. 18. Relationship of latitude and peak densities (n g^{-1} dry wt) of north Atlantic ascoglossan populations: Log_{10} (density) = 0.1109 (latitude) -2.9683, with r = .65; the relationship is highly significant (p < .01) with 33 degrees of freedom.

ANCOVA for comparison of the two major subgroups (elysiids and stiligerids) indicated that the residual variance was not significant (F = 3.49, d.f. = 1, 5), permitting comparison of separate subgroups. Slopes (F = 3.71, d.f. = 1, 11) and intercepts (F = 0.003, d.f. = 1, 12) of the two subgroups did not differ significantly, however.
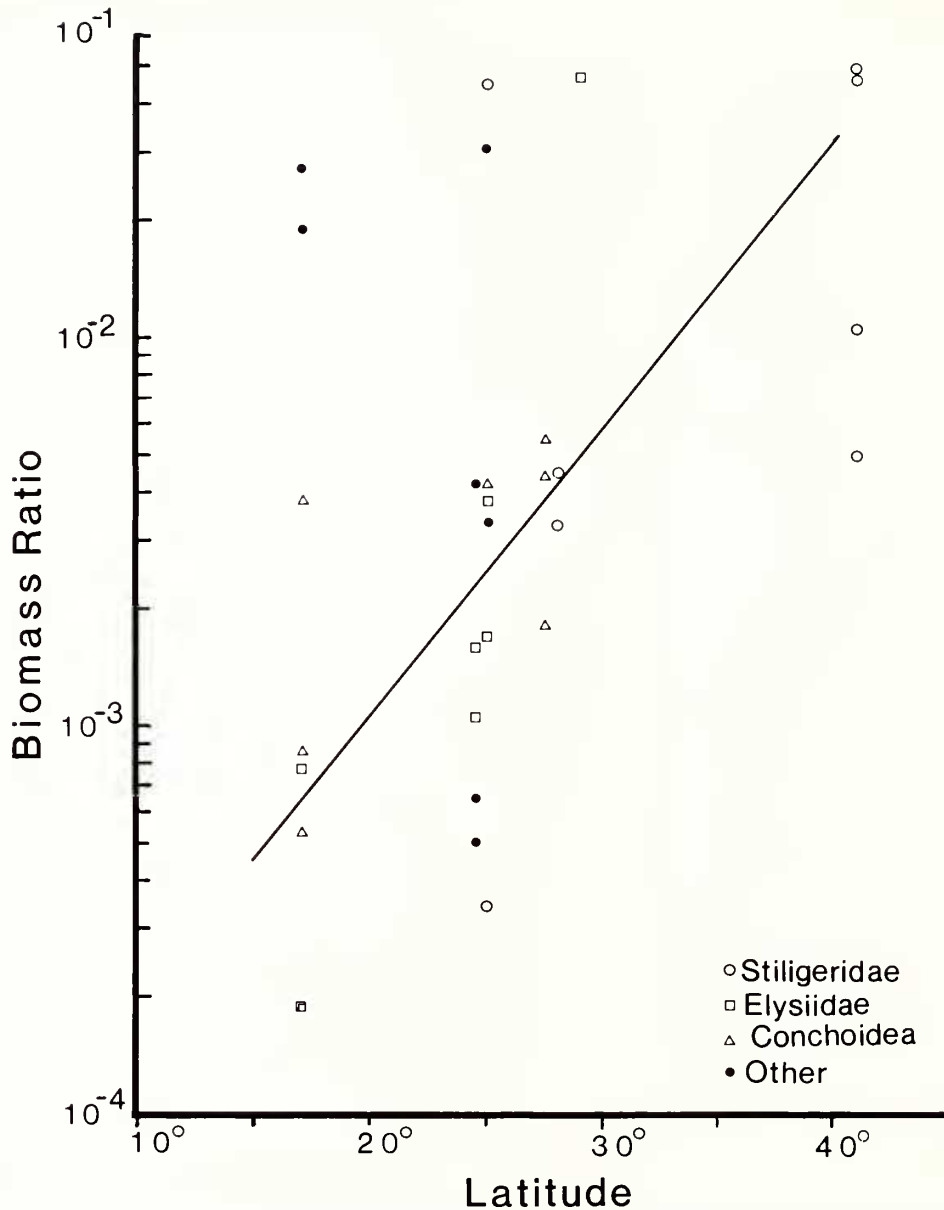
Fig. 19. Relationship of latitude and biomass ratio (dry weight of slugs: dry weight of algae) of north Atlantic ascoglossan populations: Log_{10} (biomass ratio) = 0.0744 (latitude) - 4.449, with r = .535; the relationship is highly significant (p < .01) with 28 degrees of freedom.

Peak densities and algal ash level correlated strongly and inversely (Fig. 20), with nearly a 1000-fold range in density. Densities were generally highest in mangrove habitats and lowest in reef areas (Table 2). A similar effect was observed for biomass ratio and algal ash level (Fig. 21), but a narrower range of values suggests that differences in animal size (smaller animals on low-ash algae) can affect biomass ratios.

DISCUSSION

Ascoglossans' life histories are strongly entrained upon those of their algal foods (Clark, 1975). Consequently,

their populations occur as a spatial and temporal subset of the occurrences of their algal foods, which are themselves often quite habitat-specific. This generates a highly "clumped" distribution for many species, in which relatively small populations occur, scattered within a very small percentage of the area of a potential habitat. These patterns of occurrence make quantitative sampling difficult, because the principle of fully-randomized population sampling is difficult to apply in the analysis of strongly disjunct, low-density populations. Consequently, the probability of collecting even a few slugs by standard marine sampling protocols is very small. Ascoglossans rarely appear in general community analysis tabulations, and when they do, occur as minor com-
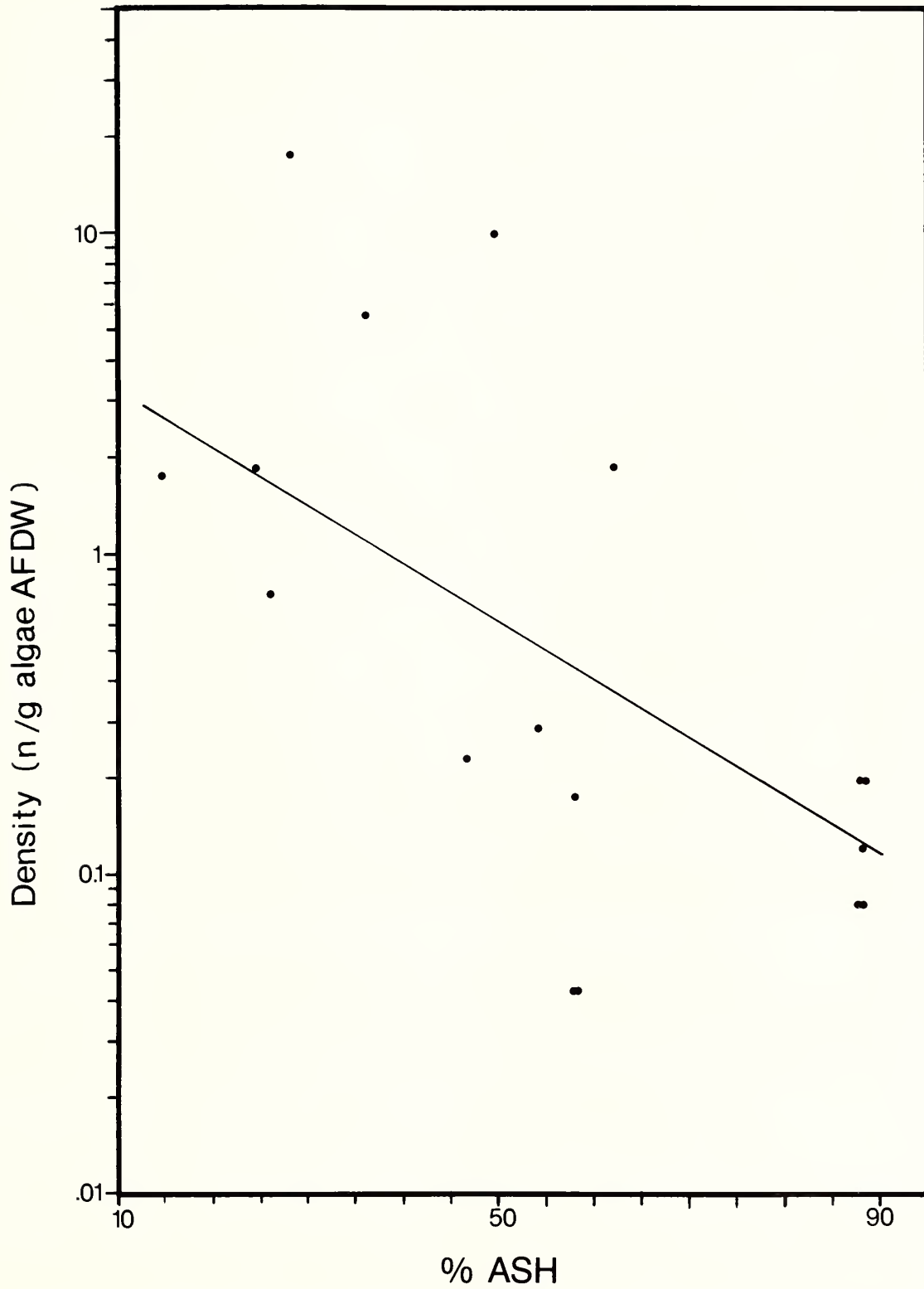
Fig. 20. Relationship of peak densities of Caribbean ascoglossans and algal ash level: Log_{10} (density) = -.01826 (%Ash) + .7002 with r = -.644; the relationship is highly significant (p < .01) with 15 d.f.
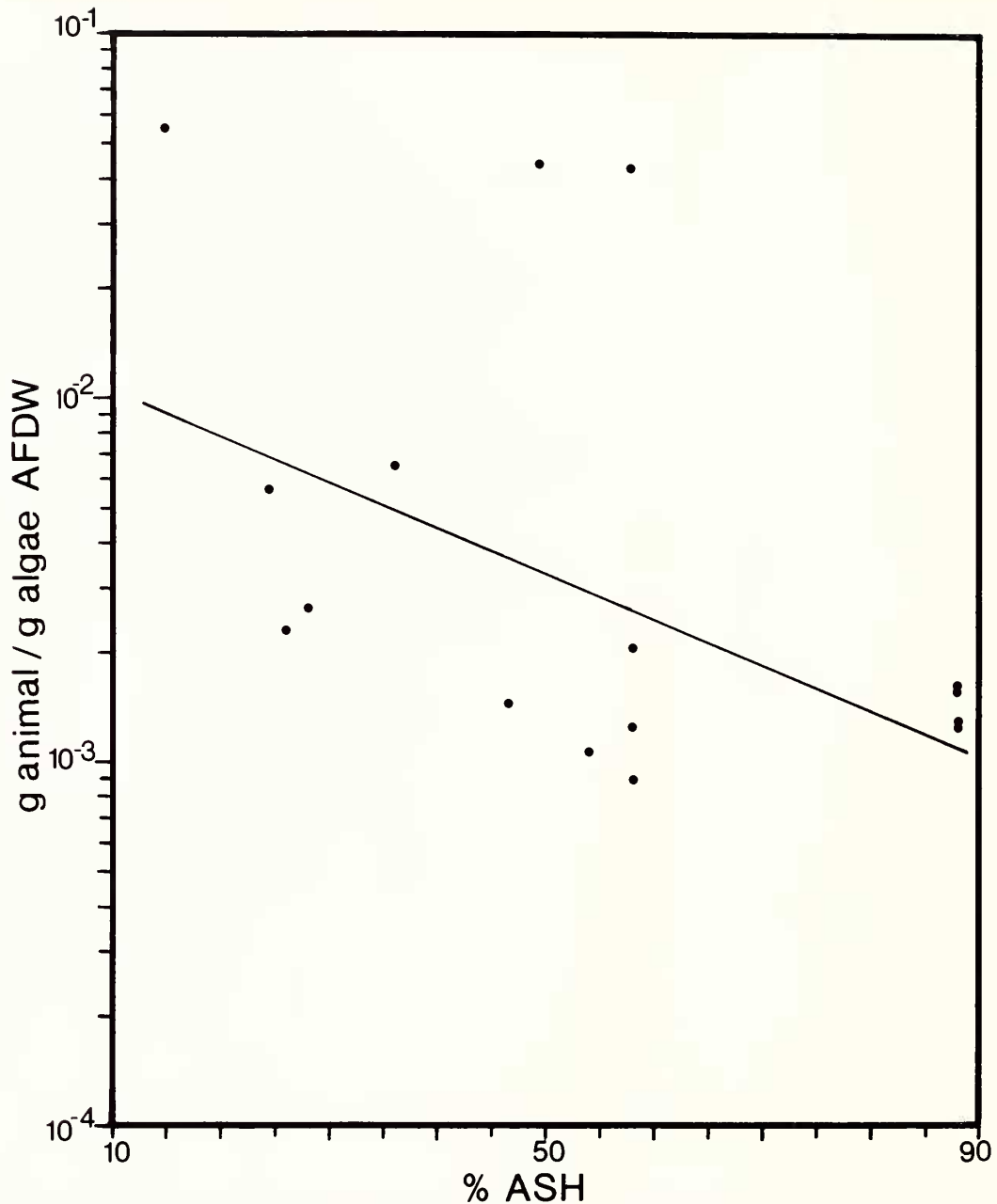
Fig. 21. Relationship of biomass ratio (dry weight of slugs/algal ash-free dry weight) and algal ash level for Caribbean ascoglossan populations: Log_{10} (biomass ratio) = -.01256 (% Ash) - 1.8649, with r = .561; the relationship is significant (p < .05) with 13 d.f.

ponents (e.g. Marsh, 1973).

There are distinct differences in the composition, population density, and diversity of Caribbean ascoglossan communities. Because ascoglossans are highly stenotrophic, the habitat is defined primarily by the algae present, which presumably vary with such environmental factors as type of substratum and nutrient availability. Ascoglossans, however, seem to be more sensitive to some environmental parameters than are their host algae, because the same algal species can occur in different communities with different ascoglossans predators (though the reverse is seldom true), and

suitable foods often occur without ascoglossan predators. There are also substantial within- and between-habitat population differences (density and biomass ratios) of ascoglossan species on the same algal species. Climatic effects also contribute to faunal differences, as shown in comparison of the *Caulerpa racemosa* communities at different latitudes. Thus, ascoglossan populations potentially serve as sensitive environmental indicators.

Factors that affect ascoglossan populations can best be defined via analysis of quantitative population differences and covariant environmental variables. In this study, two
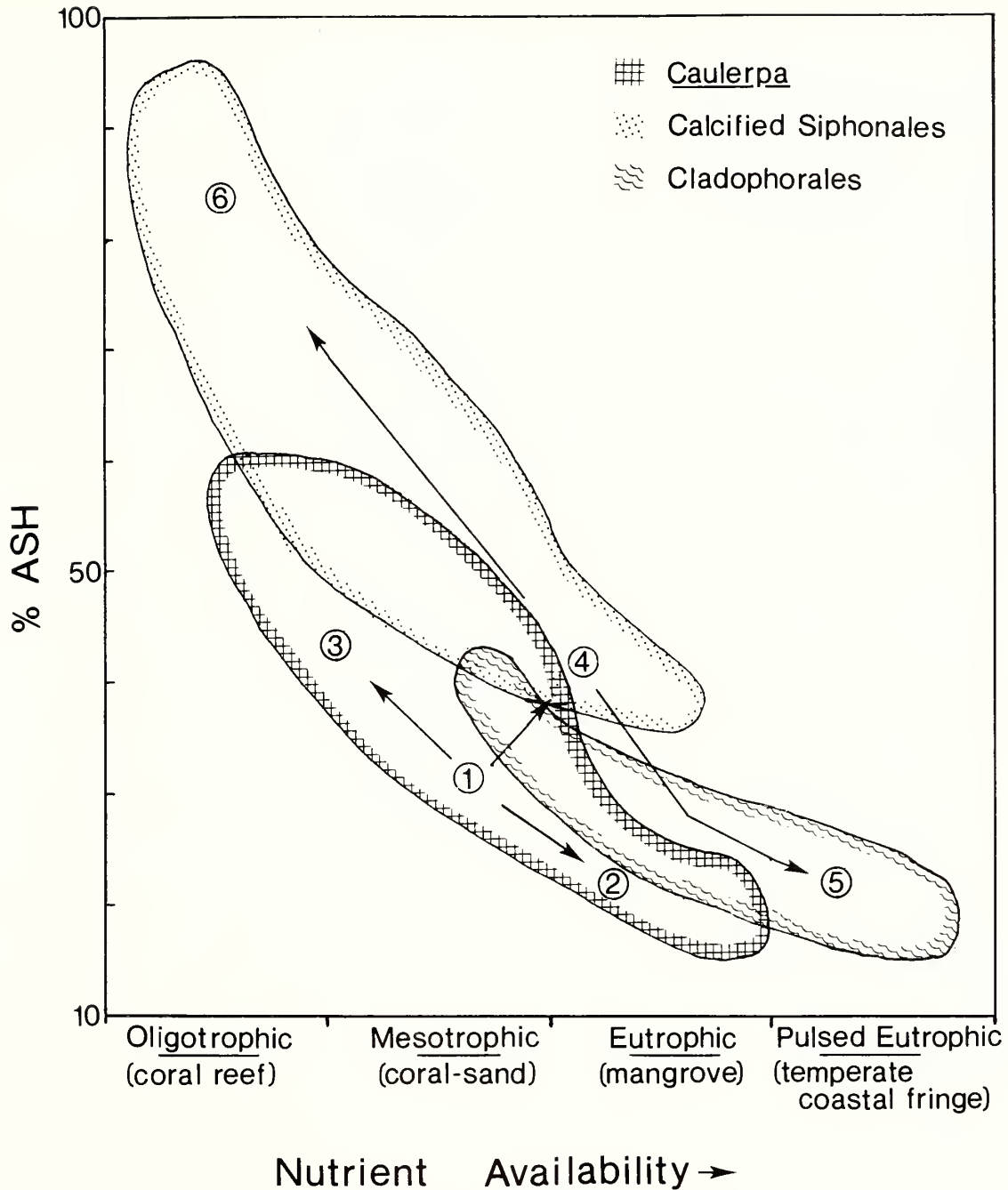
Fig. 22. Conceptual diagram of possible ascoglossan evolution in relation to feeding groups and habitats. 1 = niche of primitive burrowing Conchoidea; 2 = epimanglic Conchoidea; 3 = epilithic and reef-dwelling Conchoidea; 4 = initial adaptive radiation of unshelled ascoglossans in mangrove fringe and coral-sand habitats; 5 = radiation to Cladophorales via epimanglic filamentous algae; 6 = calciphilic radiation of elysiids, caliphyllids, and boselliids on high-ash *Halimeda* in reef systems.

variables, latitude and algal ash content, significantly correlated with variation in ascoglossan populations. Both ash content and latitude exhibit interesting possible relationships with higher taxonomic levels of the Ascoglossa and with algal morphology and taxonomy. These relationships, as discussed below, appear to provide a broad framework for considera-

tion of the major evolutionary trends among ascoglossan families.

FUNCTIONAL ALGAL/ASCOGLOSSAN ASSOCIATIONS:

Molluscan herbivores have been grouped as "func-

Table 1. Occurrence of ascoglossan species in Caribbean habitats. 1 = occurrence of species in habitat, 0 = absence. Habitat abbreviations (in order of presentation): Indian River Lagoon, FL; Sebastian Inlet Jetty, FL; Fort Pierce Jetty, FL; Bermuda Coastal Vertical Rock Face; Bermuda Causeways; Bermuda Coral-sand; Grassy Key Borrow Pit, FL; Key Largo Tidal Channel, FL; Key Largo Mangrove Channel Floor, FL; Long Key Coral-Sand, FL; Geiger Key Coral-sand; Belize Mangrove Channel Floor, Twin Cays; Belize Mangrove Pond Floor, Twin Cays; Belize Epimangle, Twin Cays; Belize Back Reef Crest; Belize Back Reef Crest; Belize Fore Reef Slope; Belize Coral-sand.

Species	Ind Riv Lag	Seb Inl Jtty	Ft Pier Jtty	Bda Cst VRF	Bda Csy VRF	Bda CS	Gras Key BP	Lar go TC	Lar go CS	Lar go MCF	Lng Key CS	Gei ger CS	Bel ize MCF	Bel ize MPF	Bel ize EPM	Bel ize BRC	Bel ize FRS	Bel ize CS	Total habitats	% habitats
Ascobulla ulla (Marcus and Marcus)	0	1	1	1	1	0	1	1	0	1	0	0	0	0	1	0	0	0	8	0.44
Berthellinia caribbea Edmunds	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	2	0.11
Lobiger souverbiei Fischer	0	1	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	7	0.39
Oxynoe antillarum Mörch	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	8	0.44
O. azuropunctata Jensen	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	4	0.22
Volvatella bermudae Clark	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0.17
Bosellia marcusi Marcus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.06
B. mimetica Trinchese	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0	6	0.33
Caliphylla mediterranea Costa	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.06
Cyerce antillensis Engel	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	1	0	1	9	0.50
C. crystallina (Trinchese)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.06
Mourgona germaineae Marcus and Marcus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0.06
Costasiella nonatoi Marcus and Marcus	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	2	0.11
C. ocellifera (Simroth)	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	0	7	0.39
Elysia evelinae Er. Marcus	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0.11
E. canguzua Er. Marcus	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.11
E. chlorotica Gould	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.06
E. flava Verrill	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	4	0.22
E. ornata Swainson	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.17
E. papillosa Verrill	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	5	0.28
E. patina Ev. Marcus	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	3	0.17
E. serca Er. Marcu	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	5	0.28
E. sp. "BL"	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0.11
E. sp. "AF"	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.06
E. sp. "GN"	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.11
E. sp. "ST"	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	3	0.17
E. subornata Verrill	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	13	0.72
E. tuca Marcus and Marcus	0	0	1	0	0	1	1	1	1	1	1	1	1	0	1	1	0	1	12	0.67
Tridachia crispata Mörch	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	10	0.56
Ercolania coerulea Trinchese	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	4	0.22
E. funera (Costa)	1	1	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	7	0.39
E. fuscata (Gould)	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0.11
E. fuscovittata (Lance)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.11
Placida kingstoni Thompson	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0.17
P. sp. "CD"	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	4	0.22
Hermaea cruciata Gould	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0.11
Aplysiopsis zebra Clark	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.06
Diversity	10	8	14	5	9	10	10	13	13	7	7	11	6	4	10	8	3	5		

tional groups" (groups of functionally similar species of broadly similar diet), but opisthobranchs have been excluded because of inadequate information on diet and ecology (Steneck and Watling, 1982). Ascoglossans form functional groups distinct from those previously recognized.

There are three major functional types of algae utilized by most Caribbean Ascoglossa. These types appear to be adapted to different nutrient regimes, which affect algal morphology and life history. Algal morphologies and life histories in turn have shaped the evolution of major ascoglossan groups at the family level.

Jensen (1983) previously noted that dietary preferences are partly shaped by algal thallus diameter. This partially reflects nutrient regimes, with more finely filamentous algae occurring in mangroves, high-energy environments, or temperate areas. Filamentous structure in these algae appears to permit rapid uptake of water column nutrients via high surface-volume ratio. Other dietary differences include presence or absence of septa, algal cytoplasmic viscosity (siphonalean algae have latex-like cytoplasm, which

coagulates on contact with sea water) and ash level.

The Ascoglossa originated on species of *Caulerpa* (Kay, 1968) and adaptively radiated in two directions, one utilizing ephemeral algae (represented primarily by Cladophorales), and the other utilizing primarily non-caulerpan Siphonales (Clark and Busacca, 1978). These radiations coincide well with gradients of nutrients and ash level (Fig. 22).

Species of *Caulerpa* are pseudoperennial (individual thalli live less than one year, but the plant as a whole is long-lived). *Caulerpa* species are intermediate in ash content (15-60%), coenocytic, almost wholly tropical, and occur predominantly in mesotrophic environments on a variety of substrata, including rock, mangrove roots, and sediments that range from organic silts to well-oxidized sand. *Caulerpa* species have well-developed absorptive rhizoids that either penetrate sediment or, in epilithic/epimanglic species, form a dense, sediment-collecting basal mat; these rhizoids function in uptake of macronutrients from the substratum (Williams, 1984). *Caulerpa* species form wound-plugs when injured (Dawes and Goddard, 1978). Wound-plug response is a necessary adaptation in plants of coenocytic structure, in order to limit loss of cytoplasm when the outer membrane is disrupted. All shelled Ascoglossa (= Conchoidea of Gascoigne, 1985) are limited to this genus (Kay, 1968), and several Caribbean elysiids feed primarily on *Caulerpa*, but very few caliphyllids or stiligerids eat *Caulerpa*. Some *Caulerpa* species appear to specialize somewhat in habitat, while others are more generalized. For example, *C. cupressoides* (Vahl) C. Agardh and *C. lanuginosa* J. Agardh occur almost exclusively on coral-sand substrata, while *C. racemosa* and *C. sertularioides* occur on a variety of sediments, mangrove roots, and on rock substrata, and occur from mangrove areas to coral reef. The more restricted species are perhaps adapted to specific nutrient regimes.

A second group of species, represented by *Cladophora, Chaetomorpha, Bryopsis*, and *Cladophoropsis,* occurs loosely associated with a variety of substrata, ranging from drift algae to mangrove roots and occasionally on rock or sediments. These algae are typically filamentous, uniseriate and septate (except the coenocytic *Bryopsis*), are highly seasonal in occurrence (Croley and Dawes, 1970) and have low to medium ash content, from 16% (Clark, unpub.) to 40% (Jensen, 1983). Growth of these algae is apparently associated with high concentrations of dissolved nutrients (often predominantly vernal), which are extracted directly from the water column (since there is seldom direct contact of the algae with sediments). These algae are colonized almost solely by ascoglossans of stiligerid morphology (*Placida, Ercolania,* and *Hermaea*). Ascoglossan recruitment on these algae occurs primarily during cooler temperatures (less than 25°C) in tropical to temperate environments, and their ascoglossan populations are thus seasonal and frequently irruptive (Clark, 1975).

The third functional group contains primarily non-*Caulerpa* siphonalean chlorophytes (*Halimeda, Penicillus, Udotea, Cymopolia, Avrainvillea*). These algae are pseudoperennial, have moderate to heavy ash level (35-95%) (including an external layer of carbonate) and occur primarily in mesotrophic to oligotrophic habitats (e.g. coral-sand to coral reef). As in *Caulerpa*, basal rhizoids extend into sediment or adhere to rock surfaces (Hillis-Colinvaux, 1980) and are associated with uptake of nutrients from the sediment (Williams, 1984). These algae also form wound-plugs when damaged (our observ.). These algae are eaten by elysiids, caliphyllids, *Costasiella*, and boselliids.

There are, of course, forms transitional between these three major groups. The thallus in *Codium* is composed of a mass of uncalcified siphonaceous filaments (Prescott, 1968). This genus is eaten both by elysiids and stiligerids, and usually occurs in mesotrophic areas of high water flow (e.g. jetty communities).

Wound-plug formation in siphonalean algae probably increases feeding effort, and its absence in septate algae probably has an important effect on stiligeriform species' feeding rates. Jensen (1981) has noted buccal regurgitation in both septate and siphonalean feeding, but this process probably has different functions in the two types of algae. On septate algae, regurgitation can work against the rigidity of the cell wall, but in siphonalean algae, it could enzymatically counteract wound-plug formation.

Differences in ash level among externally calcified algae reflect the balance between organic growth and calcium carbonate deposition. High ash content can represent either relatively low growth rate (perhaps controlled by nutrient availability) or rapid skeletal deposition (as controlled by pH-temperature regimes). In reef environments, where high algal ash levels were observed, both influences operate, as dissolved nutrient standing stocks are low (Muscatine and Porter, 1977), while high photosynthetic rates in reef areas raise pH to levels that strongly favor carbonate precipitation. Intensive predation by reef herbivores (Lewis, 1985) can also favor high ash levels in reef algae. The mangrove habitats that we have examined have very few piscine herbivores, and mangrove areas generally have nutrient concentrations relatively high for tropical marine systems (Lugo and Snedaker, 1974).

In uncalcified algae, ash level more likely reflects the level of organic components of the cytoplasm: low-ash algae provide more nutrients for a given level of feeding effort. In either case, however, ash level provides a useful index of feeding effort.

Waugh and Clark (1986) found that feeding rates of *Elysia tuca* (as indicated by kleptoplastid uptake) were lower in animals that fed upon high-ash *Halimeda incrassata* than animals that ate low-ash *H. discoidea* Decaisne. Among the species of *Halimeda* we have examined, interutricular calcification also appears to negatively correlate with utricle diameter and degree of predation by elysiids. *Halimeda incrassata* and *H. discoidea*, for example, are relatively heavily grazed and have large utricles, while *H. monile* (Ellis and Solander) Lamouroux and *H. tuna* (Ellis and Solander) Lamouroux have small utricles and support very sparse ascoglossan populations (see Hillis-Colinvaux, 1980, Fig. 17, for relative dimensions of *Halimeda* utricles). *H. cuneata* has the lowest known ash content (33%) within the genus (Böhm, 1973). Though we have no data on predation on this species, Hillis-Colinvaux (1980, Fig. 36) illustrates a specimen of *H.*
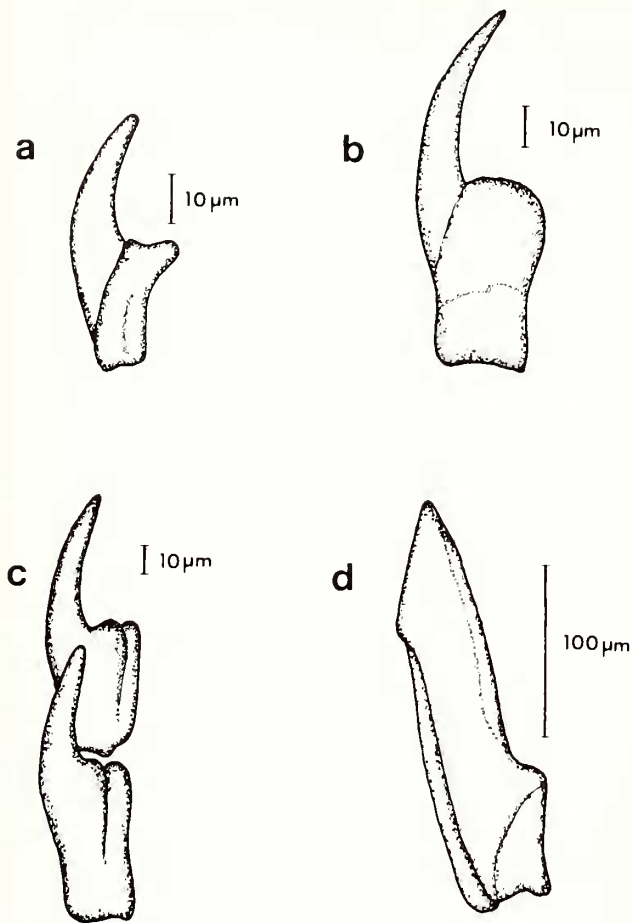
Fig. 23. Comparison of teeth of calciphilic species, showing *Halimeda*-spur (A, B, C) with caulerpivorous species (D) of *Elysia*. A = *E. papillosa;* B = *E. flava;* C = *E. tuca;* D = *E. subornata*. A, B, and E are from Clark, 1984; C is from Jensen and Clark, 1986.

cuneata with especially dense ascoglossan feeding tracks (probably of a *Bosellia*).

Caribbean elysiids that feed primarily on calcified algae (*Elysia tuca, E. flava* Verrill, *E. papillosa, E. patina* Marcus) often have a spurlike tip on the radular tooth (Fig. 23), while those that feed primarily on less-calcified algae [*E. subornata, E. ornata* (Swainson), *E.* sp. "AF"] have teeth with a broad tip. This "*Halimeda* spur" appears necessary to pierce the narrow utricles of *Halimeda* through the interutricular carbonate matrix.

The high densities noted for stiligerids, particularly in high latitudes, suggest that feeding effort is lower, and consequently growth and reproductive output are higher, for species feeding on septate, low-ash algae. Unfortunately, we have no data for high-latitude algal ash levels, but the biology of ascoglossans that eat high-ash foods suggest that feeding effort can constrain life history patterns. The transient, irruptive cycles of stiligerids (Clark, 1975) are probably unsupportable on algae of high ash content or siphonaceous structure because of lower feeding rates. Thus far, we have observed no examples of such cycles on siphonalean algae. Biomass

ratios above 1% often lead to massive destruction of algal food resources in high latitude populations (Clark, 1975), but this overgrazing apparently does not occur on siphonalean algae.

Kleptoplastid retention is apparently absent among the Conchoidea, is relatively common among ascoglossans that feed upon high-ash algae (Elysiidae), and uncommon among those feeding upon low-ash algae (e.g. Stiligeridae). The energetic benefit of kleptoplastid maintenance would be greatest in species whose energy intake is limited by algal resistance to feeding. Indeed, noting the very low densities of reef populations, retention of kleptoplastids might be the only energetically feasible way that most ascoglossans can maintain populations in reef environments.

RELATIONSHIP OF ALGAL MORPHOLOGY AND PHYSIOLOGY TO ASCOGLOSSAN DIET:

Plastid morphology has been identified as one factor limiting the occurrence of kleptoplastids. Apparently, only "robust" plastids, generally spheroid in shape and usually occurring in coenocytic (siphonaceous) algae (Hinde and Smith, 1974), are able to survive ingestion and phagocytosis by ascoglossans. Plastids of septate algae (*Chaetomorpha, Cladophora*) used as ascoglossan foods are in contrast parietal, netlike, or fragmented in shape (Prescott, 1968), fragile, and break during ingestion. The functional basis for the robust nature of siphonalean plastids has not been defined. Their shape and size, however, are convergent with those of erythrocytes among a range of animal species, and we suggest that the shape and robustness of such plastids represent necessary adaptations to shear forces resulting from fluid transport in the cytoplasm of coenocytic algae, or, alternatively, that cytoplasmic streaming creates a less-controlled, less predictable intracellular environment that requires resistant plastid membranes.

Cytoplasmic streaming movements occur in Siphonales (Dawes and Barilotti, 1969), and the observed rapid uptake and transport of sedimentary nutrients by such algae (Williams, 1984) would seem to require large scale circulatory movements of cytoplasm (macrocyclosis). Further, this would explain the ecological dominance of siphonalean algae in oligotrophic environments, as sediments represent a nutrient sink and source of nutrient fixation unavailable to algae that lack rhizoidal uptake and coenocytic structure. Thus, the siphonalean algae often occupy a sediment-extractive niche similar to that of seagrasses, and several dominant siphonalean genera normally co-occur with seagrasses (Taylor, 1960). The xanthophyte genus *Vaucheria* is also sediment-associated, siphonaceous in structure, and supports kleptoplasty (Graves et al., 1979).

The simpler, less-robust plastid membrane of non-siphonalean chlorophytes could also represent adaptation to higher external nutrient levels, in that membrane simplification would facilitate exchange of nutrients and permit higher plastid metabolic rates in situations where nutrient availability is relatively non-limiting (high latitude, eutrophic or mesotrophic habitats during vernal nutrient peaks).

The growth strategy of siphonalean algae involves a

Table 2. Ascoglossan population data. (Notes: * = mean of 2 or more samples; [†]secondary derivation (see text); (a) Warmke and Almadovar, 1972; (b) Brandley, 1j984; (c) Jensen, 1975. Habitats: FPJt = Fort Pierce Jetty; TCEm = Twin Cays Epimangle; LPPR = La Parguera reef, Puerto Rico; LSMF = Lake Surprise Mangrove; Channel Floor; CBC-RC = Carrie Bow Cay Reef Crest; SRBR = Sombrero Reef Crest, FL; TC-MP = Twin Cays Mangrove Pond; GKF = Geiger Key Coral-sand; SpHr = Spanish Harbor Coral-sand; NCT = Noank, CT; PCF = Pineda Cswy, Indian River Lagoon; HD = Hellebaek, Denmark; GKBp = Geiger Key Borrow-pit).

Species	Alga	Habitat	Lat'	Date	Temp. °C	Algal Dry Wt. (g)	Ash (%)	Biomass ratio	Density n/g dry wt
CONCHOIDEA									
Ascobulla ulla (Marcus and Marcus)	Caulerpa racemosa	FPJt	27.5	3 Apr 86	29	29.6		0.00443	0.574
Berthelinia caribbea Edmunds	C. verticillata	TCEm	17	9 Jun 85		1.49	28	0.0192	12.75
Lobiger souverbiei Fischer	C. racemosa	TCEm	17	7 Jun 85	29	55.2	58	0.00086	0.018
L. souverbiei	C. racemosa	FPJt	27.5	2 Jul 85	29	13		0.00181	0.077
Oxynoe antillarum Mörch	C. racemosa	TCEm	17	9 Jun 85		55.2	58	0.00053	0.0725
O. antillarium	C. racemosa	FPJt	27.5	2 Jul 85	29	13		0.00557	0.231
O. antillarum (a)[†]	C. racemosa	LPPR	18	Dec. 61		46.1			7.052
O. azuropunctata Jensen*	C. paspaloides	LSMF	25	27 Jun 85	27	17.9	24.5	0.00423	1.39
Volvatella bermudae Clark	C. racemosa	TCEm	17	9 Jun 85		55.2	58	0.00038	0.0181
BOSELLIIDAE									
Bosellia mimetica Trinchese	Halimeda simulans	CBC-RC	17	7 Jun 85		209	88	0.00015	0.0144
CALIPHYLLIDAE									
Cyerce antillensis Engel	H. simulans	CBC-RC	17	7 Jun 85		209	88	0.00016	0.0096
C. antillensis	Penicillus dumetosus	SpHr	24.5	25 Jan 86	23	26.8		0.00066	0.037
Mourgona germaineae Marcus Marcus*	Cymopolia barbata	GK	24.5	10 Sep 85	28	83.7	54	0.0005	0.13
ELYSIIDAE									
Elysia n. sp. "AF"*	Caulerpa prolifera	TVIR	29	12 Jun 86	27	15	14.9	0.0467	1.47
E. flava Verrill	H. simulans	CBC-RC	17	7 Jun 85		209	88		0.0096
E. furvacauda Burn (b)[†]	Codium	BBA	24.5	Oct 80		6.33			0.948
E. n. sp. "BL"	H. simulans	CBC-RC	17	7 Jun 85		209	88	0.00019	0.0239
E. papillosa Verrill	P. dumetosus	SpHr	24.5	25 Jan 86	23	26.8		0.00105	0.149
E. papillosa*	Udotea conglutinata	SWC-RC	17	12 Jun 85		107	46.5	0.00078	0.122
E. sp. "ST"	P. dumetosus	SpHr	24.5	25 Jan 86	23	26.8		0.00159	0.037
E. subornata Verrill	C. paspaloides	LSMF	25	27 Jun 85	29	10.9	26	0.00171	0.551
E. subornata	C. racemosa	TCEm	17	9 Jun 85	29	15.3	62		0.719
E. tuca Marcus and Marcus	H. simulans	CBC-RC	17	7 Jun 85		209	88	0.00010	0.0239
E. tuca	H. incrassata	LSMF	25	17 May 86	26	35.1		0.00378	0.1425
E. tuca	H. incrassata	SRBR	24.5	26 Aug 86	29.5	94.9		0.00024	0.0211
COSTASIELLIDAE									
Costasiella ocellifera	Avrainvillea nigricans	TC-MP	17	16 Jun 85	30	8.6	49.5	0.0221	5.00
C. ocellifera	A. nigricans	GKF	24.5	10 Sep 85	29	5.1	36	0.0042	3.53
C. ocellifera	A. nigricans	LSMF	25	17 May 85	26	1.86		0.031	7.8
STILIGERIDAE									
Ercolania funerea (Costa)	Cladophoropsis	LSEm	25	5 Apr 86	29	5.65		0.00034	0.531
E. fuscata (Gould)	Cladophora	NCT	41	14 Jul 70	23	0.08		0.0103	723
E. fuscata	Chaetomorpha	NCT	41	10 Aug 70	23	1.51		0.00498	31.1
E. fuscata	Cladophora	PCF	28	6 Apr 86	27	1.48		0.0045	6.74
E. fuscata	Bryopsis	PCF	28	6 Apr 86	27	3.61		0.0033	5.82
Limapontia capitata (Mueller) (c)[†]	Cladophora	HD	56	18 Jun 75	17	1.85			40
Placida dendritica (Alder and Hancock)	Codium	NCT	41	20 Apr 70	18	3.89		0.0464	32.4
P. kingstoni (Thompson)	Bryopsis	GKBp	25	25 Jan 86	23	0.75		0.0447	24.2

strong component of vegetative propagation by stolonoid extension (Hillis-Colinvaux, 1980). This strategy presumably involves extensive reorganization and cytoplasmic transport, and might require mobilization of catabolic enzymes. Trench (1980) suggested that plastid "robustness" might represent resistance to (animal host) lysozymal hydrolases, but such resistance might originate in plastid resistance to intrinsic algal hydrolases. These enzymes could be unnecessary in the highly compartmentalized systems of septate algae of seasonal growth.

The effects of latitude on biomass ratio and population density could be partially due to ash levels, as calcium carbonate has an inverse thermal solubility and thus algal carbonate levels should decrease with latitude. However, other important latitudinal effects, including seasonality of nutrients and light, standing stock of dissolved nutrients,

Table 3. Possible coevolutionary adaptations of tropical algae and ascoglossans.

Algal adaptation	Possible ascoglossan response
secondary compounds	toxin tolerance; defensive sequestration; dietary selectivity
wound-plug response	buccal regurgitation, salivary enzymes
increasing ash level	radular modification; kleptoplasty
gamete satiation	facultative consumption of gametangia

levels of toxic secondary compounds, and thermal effects on metabolic rates, probably operate on ascoglossan populations.

Additional, unmeasured factors can also covary with ash content, and the effects of ash *per se* are probably exaggerated in the present study. Two effects, variation in level of toxic algal metabolites and variations in life history characteristics, probably affect our data.

POSSIBLE COEVOLUTIONARY ASPECTS OF ASCOGLOSSAN/ALGAL RELATIONSHIPS:

Toxic secondary algal metabolites are common in siphonalean algae (Norris and Fenical, 1982). Some of these are defensively sequestered by ascoglossans (Doty and Aguilar-Santos, 1970; Norris and Fenical, 1982; Jensen, 1984) and would appear non-toxic to these animals, but other toxins can inhibit recruitment, growth, and reproduction of ascoglossans. Higher levels of caulerpin and caulerpicin occur in algae preferred by Caribbean ascoglossans (Vest et al., 1983), but whether this represents response by algae to predation or ascoglossan preference for higher toxin levels is undetermined. *Mourgona germainiae* appears to defensively utilize cymopols from *Cymopolia*; however, these are physically isolated from body tissues (Jensen, 1984), and are rapidly autotoxic to animals confined in small volumes of water. *Tridachia crispata* exhibits similar auto- and allotoxicity (pers. obs.). This suggests that even defensively sequestered compounds are potentially toxic, depending on concentration. Also, the elysiids that dominate Caribbean coral reefs (*T. crispata, Elysia subornata, E. tuca, E. papillosa*) feed upon a variety of siphonalean genera (Clark and Busacca, 1978; Jensen, 1980; present study) and are habitat generalists (Figs. 16, 17). This feeding strategy, in which feeding is dispersed over several plant species with varied metabolites, could maintain dietary intake of specific metabolites below toxic levels.

Janzen (1974) has noted that nutrient-poor terrestrial communities produce exceptionally high levels of defensive compounds in apparent response to herbivore selective pressure. Such an effect should also operate in marine systems, and the most obvious parallel is the coral reef.

A review of plant-herbivore coevolution in terrestrial systems (Rhoades, 1985) provides several interesting insect-plant interactions that can parallel ascoglossan-algal relationships. A summary of possible coevolutionary aspects of ascoglossan/algal biology is presented in Table 3. One possible parallel is the pattern of gametangia production in *Halimeda*. During this process, all tissue resources are suddenly channelled into gamete production, followed by death of the entire thallus (Hillis-Colinvaux, 1980). Gametangic thalli are strongly attractive to *Elysia tuca* (Waugh and Clark, 1986), and this reproductive mechanism apparently represents a predator-satiation strategy similar to mast-fruiting in some rain forest trees and bamboo (Janzen, 1974), necessary because gametangia are formed external to the calcareous framework of *Halimeda* thalli (Hillis-Colinvaux, 1980). Gametangia formation is synchronous in *H. incrassata*, the principle food of *E. tuca,* with about 25% of thalli in localized patches gametangious during rising spring temperatures at some localities (own obs.). Hillis-Colinvaux (1980) reports, however, that asynchronous formation of gametangia is normal among *Halimeda.*

OVERVIEW OF ASCOGLOSSAN EVOLUTION:

The maximum densities and diversity of tropical Caribbean ascoglossans occur in the transition between coral-sand and mangrove habitats. This habitat is heavily colonized by sediment-associated *Caulerpa* species. We suggest that the first ascoglossans evolved in this habitat as burrowing forms (Kay, 1968; Clark and Busacca, 1978). Other major radiations involved adaptation to utilize other functional algal types, with accompanying modification in life histories (Fig. 22).

Two major evolutionary thrusts are evident. At one extreme, ascoglossans have evolved to exploit high-ash algae as found in the coral-sand habitat and especially on the coral reef. Populations in these habitats are strongly limited by algal resistance to herbivory (especially by skeletal carbonates and latex) and exist at low densities. At the other extreme, ascoglossans have very successfully exploited septate aglae in predominantly mesotrophic habitats and occur in high-density, transient populations.

The first major adaptive radiation, from sediment-associated caulerpivores, led to non-burrowing shelled Ascoglossa feeding on epimanglic and epilithic *Caulerpa* species. Transitions from burrowing to epilithic *Caulerpa* habitats occur in *Ascobulla* (DeFreese, in press; this study) and *Volvatella* (Clark, 1982), while the Oxynoidae, Juliidae, and Lobigeridae are entirely non-burrowing and are predominantly, but not exclusively, epilithic or epimanglic. Other radiations involved exploitation of septate algae, seasonally common in epimanglic habitats, by stiligeriform species, followed by adaptation to higher latitudes, and exploitation of externally calcified siphonales by caliphyllids, boselliids, and particularly elysiids. These algae are well-represented in the coral-sand habitat, and apparently reef-dwelling, kleptoplastid-retentive, calciphilic forms represent the most advanced species in this radiation.

In inshore habitats, at least, ascoglossans are probably the most significant predators on calcified Siphonales, and might have had a significant effect on evolution of these algae. Fossil Juliidae, representing the second radiation described above, are known from the Eocene (Kay, 1968), proving an ancient relationship between ascoglossans and siphonalean algae (because all shelled Ascoglossa feed only on *Caulerpa*). However, Hillis-Colinvaux (1980) considers *Halimeda* an evolutionarily conservative genus, and fossil *Halimeda*

predate known ascoglossan fossils, occurring at least from the Cretaceous and possibly Jurassic. Thus, it appears that calcification in this group preceded ascoglossan feeding and probably has not significantly increased in response to ascoglossan herbivory.

The intimacy and antiquity of the ascoglossan-chlorophyte relationship suggest that ascoglossans could have exerted important effects on the evolution of chlorophytes, selecting for increased levels of ash and secondary compounds. The low density of ascoglossans in West Atlantic reef systems, however, suggests that the current balance of ascoglossan-algal coevolution favors the algae, presumably forcing major adaptations in ascoglossan life histories, such as a predominance of direct development (Clark and Goetzfried, 1978; Clark and Jensen, 1981) and kleptoplasty. High latitude coastal regions represent an opposite trend, in that ascoglossans often have major seasonal impact on algal populations, commonly overgrazing the food supply to the point of destruction (Clark, 1975).

Important aspects of ascoglossan-algal interactions remain to be explored. Quantitation of algal metabolites, for example, might determine whether algae proximally respond to herbivory by increased toxin production, and would clarify latitudinal and habitat effects. Analysis of ash content in distinct clonal populations of algae might also help to explain patchiness of ascoglossan populations.

ACKNOWLEDGMENTS

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